DEATH OF A SALMON: AN INVESTIGATION OF THE PROCESSES AFFECTING SURVIVAL AND MIGRATION OF JUVENILE YEARLING CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA)* IN THE LOWER COLUMBIA RIVER AND OCEAN PLUME

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From 2008 to 2011, migrating acoustic-tagged juvenile yearling Chinook salmon smolts (*Oncorhynchus tshawytscha*) were detected on receivers deployed across the Columbia River and continental shelf at Cascade Head (Oregon), Willapa Bay (Washington), and Vancouver Island (British Columbia). The telemetry data were used to estimate survival and record migration parameters. These were evaluated against oceanographic and freshwater hydrologic variables in statistical and individual-based models. Plume survival was found to be variable, but daily survival rates were more constant and survival was effectively modeled as exponential decay. Correlates of early marine survival that do not have direct effects may act on plume survival by controlling the period of exposure to plume predation. In 2011, half of smolts released were exposed to total dissolved gas levels (TDG) above 120%, the water quality limit for TDG below Columbia River dams. This exposure appears to have negatively affected daily survival rates in the lower river and plume, and has important implications for a proposal to

increase the TDG limit to 125% to support spring fish passage. Finally, consistent with the critical size, critical period hypothesis of salmon production, it appears that smolts select habitat to maximize their growth as they migrate north through the plume, rather than selectively using local currents to speed their passage. These findings shed new light on perennial questions in salmon early marine ecology. They lay the groundwork for future research aimed at understanding the effects of changing oceanography and freshwater hydrology on salmon migration and survival.

BIOGRAPHICAL SKETCH

Ian G. Brosnan was born in Galway, Ireland on August 20th, 1980. He immigrated to the United States in 1986, and was granted U.S. citizenship in 1999. He attended the U.S. Coast Guard Academy from 1999 to 2003, earning a Bachelor's of Science, with High Honors, in Marine and Environmental Science. He was commissioned as an Ensign in the U.S. Coast Guard and reported to the Coast Guard Cutter KUKUI (WLB-203) in Honolulu, Hawaii, where he served for two years as a deck watch officer and military diver. In July 2005 Lieutenant Brosnan assumed command of the Coast Guard Cutter COBIA (WPB-87311), homeported in Mobile, Alabama. He subsequently served as the Congressional Affairs Officer for the Thirteenth Coast Guard District in Seattle, Washington and transferred to the Coast Guard Reserve in 2009. He earned a Master's of Marine Affairs from the University of Washington in 2010, and was a National Academies of Science Christine A. Mirzayan Science and Technology Policy Fellow on the Ocean Studies Board. He entered the Ph.D. program in Ecology and Evolutionary Biology at Cornell University in the fall of 2010.

To my wife, Meaghan, and grandfather, Ken Rodhouse.

ACKNOWLEDGEMENTS

I must first thank my two advisors, Drs. Chuck Greene & David Welch. Dr. Greene provided me the opportunity to conduct this research at Cornell University, and has been immensely helpful as my committee chair and advisor. Dr. Welch kindly allowed me to join his team at Kintama Research Services conducting telemetry-based salmon research; he has been a trusted and valued advisor on both technical and professional matters. I am deeply grateful for their insights and advice.

Drs. Pat Sullivan and Lars Rudstam kindly agreed to serve on my committee. Their advice and guidance on statistics and fisheries ecology were of inestimable value. Pat's early comments to me on individual-based modeling and structured decision making (SDM) shaped the direction of a significant part of my research and service as a Ph.D. candidate. I am grateful to Dr. Angela Fuller who gave me an initial recommendation to the structured decision making program at the National Conservation Training Center, and funded my attendance at a 2012 workshop. I am also indebted to Dr. Kiho Kim, who provided me with desk space in his lab at American University, and arranged for a visiting scholar position while I completed my dissertation in Washington, DC.

My wife, Meaghan, and my family, including Paul, Deborah, Steven, Laura, Heather, and Tom, have been tireless in their support, providing words of advice

and encouragement whenever it was needed. Paul and Deborah separately advised that I write and attempt to publish as I went. That advice served me well, and played no small role in my success as a graduate student. Many others provided advice, fellowship, and camaraderie through the Ph.D. process, including the members of the Greene lab, Dr. Bruce Monger, Dr. Louise McGarry, Erin Meyer-Gutbrod, and Rob Levine, my colleagues and Ph.D. cohort in the Department of Ecology and Evolutionary Biology, the Kim Lab, and the faculty and staff at American University. I am also grateful to the countless friends and colleagues, too many to name here, that have provided words of encouragement, advice, or a sympathetic ear during this journey.

Finally, the Department of Defense, through the National Defense Science and Engineering Graduate Fellowship program, provided support for my first three years at Cornell. In my final year, support came from the National Science Foundation under Award No. 1235751, and the Post-9/11 GI Bill. Funding for research was provided by the Atkinson Center for a Sustainable Future, Bonneville Power Administration, and the U.S. Department of Energy. Cornell University Graduate School and Kintama Research Services provided funds to travel and present research results at several scientific meetings.

TABLE OF CONTENTS

PREFACE

It is difficult to pinpoint the start of this Ph.D. journey. It may have something to do with being raised by marine scientists. Certainly, they influenced my choice to join the Coast Guard and pursue marine science as an undergraduate major. However, it was a copy of *Advances in Conservation Oceanography: New Tagging and Tracking Technologies and Their Potential for Transforming the Science Underlying Fisheries Management*, sent by my mother, that sparked my interest in acoustic telemetry and sent me down this particular path. I had known the lead author of the paper, Chuck Greene, from my childhood summers at Friday Harbor Labs. When I read the paper, I was a Master's candidate at the University of Washington and I called Chuck to discuss opportunities in conservation oceanography whilst I was driving out for a kayaking trip at Neah Bay, Washington. Shortly afterwards he invited me to attend his Marine Bioacoustics course at Friday Harbor Labs. In addition to providing funding, he connected me with David Welch, President and CEO of Kintama Research Services. At the time, David was actively engaged in acoustic telemetry-based salmon research on the Columbia River and U.S./Canadian Pacific shelf and was kind enough to bring me onboard.

With Chuck and David's guidance, I began by researching the effects of the Columbia River plume on early marine survival of juvenile salmon. That work led to the analysis of the effects of dissolved gas on river and early marine survival

during the 2011 La Niña-driven flooding in the Columbia River. My interest in individual-based models arose from a chance remark by Pat Sullivan, one of my committee members, that an IBM might be an appropriate analytical approach to some of my questions. Following his comment, I pulled Volker Grimm and Steven Railsback's 2005 text on individual-based modeling and ecology from Mann Library, and was entranced. I committed to developing an IBM as a part of my research, and later had the opportunity to attend Grimm and Railsback's IBM workshop in Germany.

Many journeys take unexpected directions, and it was another remark from Pat that led me to structured decision-making (SDM), the application of decision science to natural resource management. In the spring of 2012, I had committed to limiting my course load so that I could focus on research. However, just ahead of the semester's start, Angela Fuller announced that she would be teaching an introduction to SDM course through the USGS co-op unit. Although it pained me to do so, I knew I could not pass up the opportunity and I enrolled in the course. That course ultimately led to apprenticing, and then coaching, SDM workshops at the National Conservation Training Center. I have found that I really enjoy combining elicitation and coaching with technical modeling in these collaborative, participative processes, and it is work I hope to continue beyond graduate school.

This is the last piece of my dissertation to be written, giving me cause to reflect

on my decision to pursue a Ph.D., and what it has meant. The opportunity costs were high – starting over after a successful career as a sea-going officer, trading a salary and benefits for a stipend, living apart from Meaghan again, working long days and many weekends, and squeezing work into most of my vacation days.

On the other hand, few people have the luxury of pursuing a Ph.D., and I have not lacked funding and support. I was largely free to write my own schedule, and I have opportunities in post-doctoral employment to set my own course (ultimately, that may be the true value of a Ph.D.). I enjoyed having the opportunity to read widely in marine science ahead of my qualifying exam, and then immerse myself in work that was truly my own. I'm pleased to have developed strong quantitative skills, which is one reason I went back to graduate school. I was surprised that I needed to also develop programming skills, but enjoyed that as well. I've also discovered a passion for coaching and elicitation of values in model-supported collaborative decision-making. Thus, in spite of the challenges, pursuing a Ph.D. was the right choice.

INTRODUCTION

Pacific salmon have significant social, ecological, and economic value along the U.S. Pacific Northwest and western Canadian coasts. Their early survival, particularly their early marine survival, is believed to play a key role in determining the number of adult salmon that return to spawn in their natal streams, or be caught by fishers for consumption and traditional cultural uses. As a consequence, evaluating the effect of oceanographic and environmental covariates on early survival and migration has been an important long-term research focus of Pacific salmon ecologists. Although juvenile salmon have been well studied, persistent access in the marine environment has been limited by weather and cost constraints on trawl surveys. Thus, new insights are possible with the development of miniaturized electronic tags with unique acoustic transmissions that permit sustained, direct measurement of survival and migration in estuaries, river plumes, and the coastal ocean.

This dissertation contains three chapters that examine survival and migration of acoustic-tagged juvenile yearling Chinook (*Oncorhynchus tshawytscha*) salmon, commonly referred to as smolts, in the lower Columbia River and ocean plume. The first two chapters examine the role of the marine and river environments on survival using a mark-recapture statistical framework. The third chapter departs from this framework to evaluate two migratory strategies using an individual-

based model. Each chapter is briefly introduced here, and has its own in-depth introduction.

Chapter 1 evaluates the influence of the river and ocean environment on smolt survival in the Columbia River plume, 2008 to 2011. The use of survival measured directly in the Columbia River plume, rather than estimates of smolt-to-adult returns made 1 to 5 years and many thousands of kilometers after smolts have experienced the conditions of their early marine life history, marks an advance over previous research into early marine survival. The main finding is that ocean conditions appear to affect plume survival by mediating plume residence time. This chapter was published in 2014 in Marine Ecology Progress Series (Vol. 496: 181-196), under the title, *Evaluating the influence of environmental factors on yearling Chinook salmon survival in the Columbia River plume (USA)*. It was a contribution to a Theme Section entitled, 'Tracking fitness in marine vertebrates.'

Chapter 2 examines the survival effect of exposure to high levels of total dissolved gas (TDG) on yearling Chinook smolt survival. Supersaturation (TDG > 100%) below dams is usually the result of spilling water rather than passing it through turbine powerhouses. This is done voluntarily to reduce physiological impacts of dam passage, and may improve smolt-to-adult returns (SARs). However, exposure to high levels of TDG has physiological effects that may

result in smolt death, or reduced fitness. Thus, spill is permitted up to the level that total dissolved gas below the spillways is less than, or equal to, 120%. This limit may be waived during periods when the river flow exceeds the capacity of the powerhouses.

Such an exceedance occurred in 2011 as a result of *La Niña*-driven spring flooding. TDG levels surpassed 130% below Bonneville Dam and appear to have affected survival rates of smolts in the lower Columbia River River and plume. Survival effects below Bonneville Dam have never been examined, and the results in this chapter were used by the Northwest Power Planning Council's Independent Scientific Advisory Board in their evaluation of the merits of a proposal to evaluate the effects of elevated spill (up to 125% TDG) on SARs over ten years, at an approximate opportunity cost of 1.1 Billion USD.

Chapter 3 evaluates two strategies smolts may adopt during their migration through the plume, a region of relatively low smolt survival. In the first strategy, smolts migrate north, selecting habitat that offers the greatest growth opportunity. This is consistent with the critical size, critical period hypothesis that explains smolt-to-adult return rates as a function of two growth-related mortality periods during the early marine life history: predation-based mortality period at ocean entry, followed by starvation-based mortality over the first winter.

Under the second strategy, smolts selectively use coastal currents to minimize head current while migrating north. This strategy should speed their passage through the plume environment, and would be consistent with the behaviour of adults and juveniles in river settings, behaviour that is difficult to observe directly in the marine environment. Unlike Chapter 1 and 2, where analysis was conducted using mark-recapture statistics, Chapter 3 relies on an individual-based model specifically developed to evaluate the hypothesized strategies.

CHAPTER 1

EVALUATING THE INFLUENCE OF ENVIRONMENTAL FACTORS ON YEARLING CHINOOK SALMON SURVIVAL IN THE COLUMBIA RIVER PLUME (USA)

Abstract

The impact of oceanographic processes on early marine survival of Pacific salmon is typically estimated upon adult return, 1 to 5 yr after ocean entry, and many 1000s of kilometers after initial exposure. Here, we use direct estimates of early marine survival obtained from acoustic-tagged yearling Chinook salmon (*Oncorhynchus tshawytscha*) that entered the Columbia River plume (USA) after migrating down the river and then north to the coastal waters off Willapa Bay, Washington. Plume residence time averaged 7 d, and was of such short duration that predation, rather than feeding and growth conditions, was the likely primary cause of mortality. Plume survival ranged from 0.13 to 0.86, but was stable when scaled by plume residence time, and we find that a simple exponential decay model adequately describes plume survival. Plume survival, and perhaps adult returns, could be improved by reducing plume residence time if the drivers controlling residence time were amenable to management control. However, we show that a statistical model of plume residence time that includes only sea-surface temperature far outperforms models that include river discharge and

coastal upwelling. Timing hatchery releases using marine environmental forecasts could potentially improve smolt survival by minimizing their residence time in regions of poor survival. Acoustic telemetry may be used to evaluate the value and effectiveness of such approaches.

Introduction

The Columbia River basin once supported large stocks of Pacific salmon, but their abundance has declined significantly under the combined effects of overfishing, damaging land-use practices, hydropower development, periodically unfavorable conditions for salmon survival in the North Pacific Ocean, and hatchery supplementation that accompanied the industrialization of the Pacific Northwest (National Research Council 1996, Mantua et al. 1997, Coronado & Hilborn 1998). Since the passage of the Endangered Species Act in 1973, five of the seven evolutionarily significant units (ESUs) of Chinook salmon (*Oncorhynchus tshawytscha)* in the Columbia River basin have been listed as 'Threatened' or 'Endangered' and significant effort has been directed towards understanding the ocean ecology of salmon in the hopes of restoring depleted stocks (Brodeur et al. 2003, USNARA 2012).

Pearcy (1992) suggested that the number of juvenile salmon returning to spawn in their natal streams as adults may be established during the cohort's first month

at sea, a ‘critical period’ of early marine survival. The possibility of predicting, and perhaps influencing, adult returns by elucidating the drivers of early marine survival has subsequently been an important focus for salmon ecologists. Numerous environmental variables have been examined for potential relationships with early marine survival. Although some variables lack clear mechanistic links to survival, they are generally related to feeding and growth opportunities, predation, and the effect of experiences in the river on subsequent fitness.

The annual transition to dominant northerly winds in spring, the ‘spring transition’, drives upwelling of cold nutrient-rich waters that support phytoplankton blooms and advect lipid-rich cold-water copepod species into the marine waters of Oregon and Washington, displacing relatively lipid-poor warm-water species and providing a food web input believed to be favorable for juvenile salmon growth (Huyer et al. 1979, Hickey & Banas 2003, Peterson & Keister 2003, Peterson & Schwing 2003, Schwing et al. 2006). The timing of ocean entry of juvenile salmon relative to the spring transition has been proposed as a driver of early marine survival (Logerwell et al. 2003, Scheuerell et al. 2009; but see Tomaro et al. 2012).

DeRobertis et al. (2005) and Morgan et al. (2005), in companion papers, directly examined the potential relationships between feeding and survival by sampling

juvenile salmon and their prey at tidally driven Columbia River plume fronts and in the adjoining plume waters and coastal ocean. They found that the fronts aggregate salmon prey, but found little evidence that juvenile salmon take advantage of the feeding opportunities at the fronts, potentially due to their ephemeral nature. While juvenile salmon may not take advantage of unique feeding advantages presented by the fronts, field sampling and bioenergetics modeling have indicated that they are not food limited in the plume region (Brodeur et al. 1992, Morgan et al. 2005).

Although they may not be food limited, juvenile salmon are subject to predation. Emmett et al. (2006) describe the seasonal migration of predatory Pacific hake (*Merluccius productus*) into coastal waters off the Columbia River and note that improvements in marine survival of juvenile salmon beginning in 1999 were coincident with a decrease in predator fish abundance. Emmett & Sampson (2007) used a trophic model to demonstrate that high numbers of Pacific hake could account for high mortality of juvenile salmonids leaving the Columbia River. Collis et al. (2002) describe high and increasing proportions of juvenile salmonids in the diets of Caspian terns (*Sterna caspia*) and double-crested cormorants (*Phalacrocorax auritus*) from April into May. Colonies studied by Collis et al. (2002) on Rice Island in the mid-Columbia River were subsequently successfully encouraged to nest on East Sand Island (adjacent to the plume), reducing the proportion of their diet that consisted of juvenile salmon (Roby et al. 2002), but potentially increasing predation pressure in the plume. Turbidity in the plume may

offer some relief as it has been shown to reduce predation on juvenile salmon (Gregory & Levings 1998, DeRobertis et al. 2003), despite reducing predator avoidance behavior (Gregory 1993).

There may also be latent effects of the river experience on early marine survival; Budy et al. (2002) and Schaller & Petrosky (2007) examined the effects of dam passage and concluded that there is evidence that the hydrosystem experience results in mortality that is delayed into early marine residence. Additionally, as a consequence of water being spilled over the dam faces (to reduce the physical and physiological stressors juveniles are exposed to during dam passage), air is entrained in the river, resulting in gas supersaturation below the dams. Exposure to supersaturated river water may result in gas bubble trauma in juvenile salmon (Bouck 1980), and, even when exposure is non-lethal, it may reduce their fitness and increase their susceptibility to predation (Mesa & Warren 1997).

Other environmental variables that have been associated with early marine survival do not have mechanistic explanations as clear as those described above. Ryding & Skalski (1999) and Cole (2000) linked survival with sea-surface temperature (SST), although when SST was examined in a suite of coastal oceanographic variables, including upwelling, wind mixing, mixed layer depth, sea level, and the timing of the spring transition, it was not proven to be a dominant driver and is often an inconsistent predictor of adult returns (Hobday &

Boehlert 2001, Koslow et al. 2002, Scheuerell & Williams 2005, Burke et al. 2013). Burla et al. (2010a) considered the effect of plume size and position, which are largely shaped by river discharge and wind-driven current, on juvenile survival and found no significant relationship with Chinook salmon returns and only a very weak relationship with steelhead salmon (*Oncorhynchus mykiss*) returns.

Here, we combine 2 novel approaches to gain insight into yearling Chinook survival in the Columbia River plume region, in their first period of marine residency. First, we use acoustic telemetry, which permits direct empirical measures of early marine survival to be evaluated against the environmental conditions experienced by tagged smolts (e.g. Rechisky et al. 2009, Moore et al. 2010, Welch et al. 2011, Thorstad et al. 2012, Melnychuk et al. 2013). This improves on the current approach to identifying critical environmental variables, which primarily relies on correlating them with smolt-to-adult return rates estimated over 1 to 5 yr and many 1000s of miles after exposure.

Second, we recognize that the plume is a region where occupancy is short and predators are rich, and thus it is conceivable that plume survival of telemetered smolts is regulated by their period of exposure (i.e. plume residence time) and that variables associated with survival, but lacking a direct link, may be acting on survival by influencing residence time. Therefore, in our analysis, we (1) evaluate

the ability of a simple exponential decay model, equivalent to those used to model the decay of radioactive elements, to describe plume survival data for tagged yearling Chinook, (2) use the model residuals in survival analyses to examine whether measures of biological productivity or gas supersaturation levels, which may directly affect survival, would add additional predictive power to the model, and (3) evaluate the effect of 3 variables, potentially related to survival but lacking clear mechanistic links, on plume residence time. These variables are SST, river discharge and wind-driven surface currents, the latter reflected in the coastal upwelling index. Finally, in light of our findings, we briefly discuss manipulating the dynamics of the Columbia River plume through flow control as a potential mechanism for improving plume survival of salmon (Jacobson et al. 2012).

Materials and Methods

Acoustic tagging and tracking

From 2008 to 2011, yearling Chinook (*Oncorhynchus tshawytscha*) from the Columbia River basin were surgically implanted with uniquely coded VEMCO V7-2L (7x20 mm, 1.6 g in air, 69 kHz transmission frequency) acoustic transmitters and then tracked as they migrated down the Columbia River and north along the continental shelf (Figure 1.1). Yearling Chinook were used because several evolutionarily significant units in the Columbia River are listed as ‘Threatened’ or ‘Endangered’ under the USA Endangered Species Act and because their larger

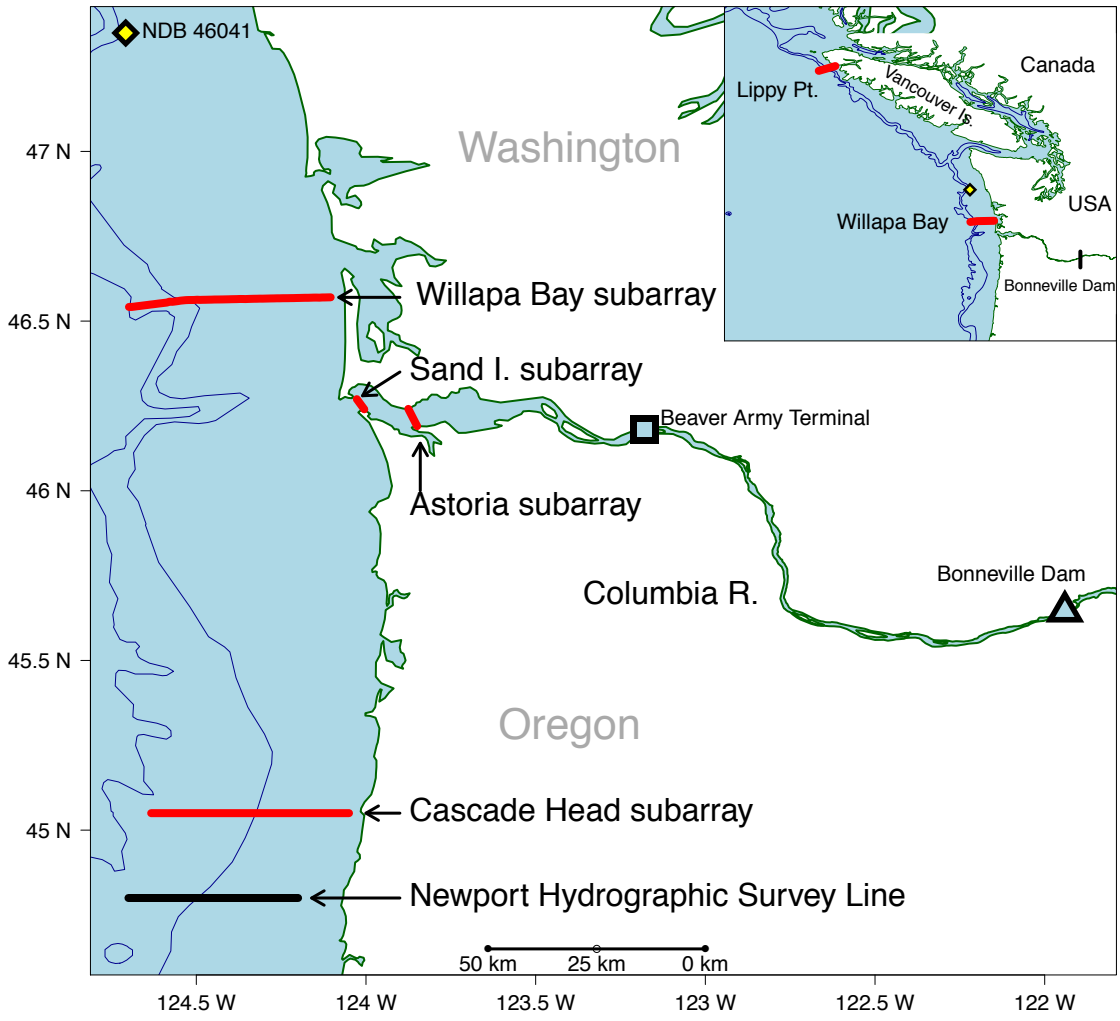

Figure 1.1. Study region. The red lines mark the named telemetry sub-arrays. Contour lines mark the 200 m and 500 m isobaths.

size reduces their tag burden. Although all groups of fish tagged and released for this study had a common migratory route in the lower river, estuary, plume, and coastal ocean, they followed 3 different migratory paths to the lower river, depending upon their origin and handling. They include Columbia run-of-the-river (CR) groups, Snake run-of-the-river (SR) groups, and Snake River transport (ST) groups (Table 1.1). In 2011, CR fish were identified as upper-Columbia (UC) or mid-Columbia (MC) using genetic stock identification (Table 1.1). Run-of-river groups were collected from hatcheries or at dams in their respective rivers, and then released to migrate to the ocean. Transported groups were collected from a hatchery or from Lower Granite Dam in the Snake River basin and then transported via truck or barge to below Bonneville Dam, the final dam on the Columbia River. With the exception of a unique early-April release of a group of transported fish in 2009, all releases occurred between late-April and late-May to minimize potential effects of emigration timing (Muir et al. 2006); release dates are reported in Table 1.1. The methods summarized here are also available in uncondensed reports to the Bonneville Power Administration (Porter et al. 2009b, 2010, 2011, 2012a,b) and in Rechisky & Welch (2010).

In 2008 and 2009, the CR groups were reared at the Cle Elum Supplementation and Research Facility on the Yakima River (a tributary of the Columbia River), but were captured, tagged, and re-released in 2 sub-groups 6 d (2008) and 7 d (2009) apart at the downstream Chandler Juvenile Monitoring Facility (CJMF). This was done to avoid the significant mortality, and thus reduced sample size,

Table 1.1. Group names, release dates, sample sizes, fork length (FL) range, proportion (%) of the population represented by the size range tagged, and estimates of plume survival for acoustic-tagged Chinook smolts released in the Columbia (CR) and Snake Rivers (SR), or Snake River-sourced smolts that were transported and released below Bonneville Dam (ST). Chinook smolts released in the Columbia River in 2011 were identified as mid-Columbia (MC) or upper-Columbia (UC) using genetic stock identification. The ST_09ER (early release) group, shown for reference, was excluded from the analysis.

Year	Group	Release dates	No. of Fish	FL Range (mm)	Percent of Population	Median plume entry date	Plume survival (SE)
2008	SR_08	25 April & 2 May	395	130-159	10	28 May	0.41 (0.07)
	ST_08	17 May & 23 May	199	131-159	10	26 May	0.52 (0.08)
	CR_08	15 May & 21 May	378	129-158	72	29 May	0.38 (0.06)
2009	SR_09	4 May & 11 May	389	130-164	68	30 May	0.53 (0.16)
	ST_09	27 May & 3 June	392	130-167	68	31 May	0.86 (0.14)
	ST_09ER	17 April	196			27 April	0.78 (0.15)
	CR_09	18 May & 25 May	393	130-159	69	2 June	0.36 (0.12)
2010	SR_10	17 – 24 May	383	130-167	74	4 June	0.69 (0.11)
	ST_10	18 – 26 May	406	130-171	74	27 May	0.58 (0.07)
	CR_10	28 April – 13 May	790	130-215	88	14 May	0.41 (0.05)
2011	SR_11	23 April – 28 May	80	132-168	78	25 May	0.25 (0.07)
	ST_11	3 May – 22 May	200	130-165	71	24 May	0.13 (0.03)
	UC_11	23 April – 28 May	386	130-170	78	21 May	0.31 (0.04)
	MC_11	23 April – 28 May	59	131-168	74	11 May	0.22 (0.07)

that occurs between these 2 facilities (Yakima Nation 2011). The SR and ST groups consisted of yearling Chinook reared at the Dworshak National Fish Hatchery (DNFH) on the Clearwater River (a Snake River tributary). The SR groups were released upstream of DNFH in 2 sub-groups 7 d apart. The ST groups were trucked to Lower Granite Dam and then placed in a barge for transport and release below Bonneville Dam in 2 sub-groups 6 d apart. There was also a single early transport release in 2009 (ST_09ER).

In 2010, the CR group consisted of hatchery- and wild-origin smolts (62% had fin clips) collected and tagged at the John Day Dam (Columbia River) before being released 42 km upstream in small sub-groups over 15 d. The Snake River groups consisted largely of hatchery-origin fish (97% had fin clips) that were collected and tagged at Lower Granite Dam and released in the tailrace over 8 d, or

transported and released below Bonneville Dam in the lower Columbia River over 9 d. Unlike 2008, 2009, and 2011, the stocks of origin for fish tagged in 2010 are unknown. We have assumed that smolts collected at John Day Dam originated in the Columbia River (although some could be Snake River smolts) and those collected at Lower Granite Dam were of Snake River origin. We have also assumed that these fish are yearling Chinook, but since they were not known to be hatchery fish (as in 2008 to 2009) or genetically identified (as in 2011), it is possible that a proportion were holdover fall type yearlings.

In 2011, juveniles in the CR and SR groups were captured and tagged at Bonneville Dam and then released in the tailrace over 14 and 7 d, respectively. Genetic stock identification was used to distinguish the spring Snake, mid- and upper-Columbia smolts used in the analysis (Porter et al. 2012b). The ST group fish were collected at Lower Granite Dam and transported for release below Bonneville Dam in 2 groups 8 d apart.

The surgical protocol for implanting the VEMCO V7-2L acoustic tag included sedation, anesthetic induction, tagging, and recovery. Briefly, fish captured for tagging were allowed to acclimate to their holding tank, and food was withheld for approximately 24 h prior to surgery. Fish were sedated with a 20ppm dose of tricaine methane sulphonate (TMS or MS-222), and anesthetic induction was accomplished in a bath containing 70 ppm TMS. Once they reached Stage IV

anesthesia, smolts were placed ventral side up, and their gills and mouths gently irrigated with a water tube. An incision to accommodate the tag was made on the mid-ventral line, and the tag was inserted into the abdominal cavity. Incisions were closed with sterile monofilament absorbable suture, and fish were transferred to a recovery tank for at least 24 h before release.

Environmental data

Researchers have identified a number of environmental variables that may be related to the early marine survival of juvenile salmon. Using current literature as a guide, we identified 6 variables with publicly available datasets for exploratory analysis. These were timing of the biological spring transition (Koslow et al. 2002, Logerwell et al. 2003, Tomaro et al. 2012, Burke et al. 2013), cumulative upwelling prior to ocean entry (Schwing et al. 2006), turbidity (Gregory & Levings 1998, DeRobertis et al. 2003), SST (Ryding & Skalski 1999, Hobday & Boehlert 2001, Koslow et al. 2002, Logerwell et al. 2003, Burke et al. 2013), and upwelling and river discharge (Budy et al. 2002, Schaller & Petrosky 2007, Burla et al. 2010a). We lacked predator data, but hypothesized that if predation was the primary driver of survival, then survival could be related to period of exposure, i.e. plume residence time. Finally, flooding in the Columbia River basin in 2011 resulted in high levels of involuntary spill at Bonneville Dam, supersaturating the river below the dam with dissolved gas and raising our interest in the effect of physiological damage resulting from exposure to supersaturated water on

subsequent plume survival (Mesa & Warren 1997, Mesa et al. 2000, USACOE 2011). We performed an initial exploration of the data with pairwise plots and used Pearson correlation coefficients to identify strongly collinear variables (Pearson correlation coefficient ≥ 0.95).

Coastal upwelling (UP), 2 and 4 wk cumulative upwelling (CU2, CU4). Daily upwelling index values at 48° N (cubic meters per second per 100 meters of coastline) were obtained from the NOAA Pacific Fisheries Environmental Laboratory (www.pfeg.noaa.gov/). Values were averaged over the period between plume entry and plume departure (see 'Analysis' section for how entry and departure dates were determined) for each salmon group in each year and cumulative upwelling was calculated for the 14 and 30 d periods prior to plume entry of each group in each year.

Biological spring transition (BST). We used transition dates for 2008 to 2011 that were calculated using the Peterson method and obtained through Columbia River Data Access in Real Time (DART; www.cbr.washington.edu/dart/). The Peterson method identifies the BST date as the day when cluster analysis of copepods sampled during biweekly research cruises at the hydrographic baseline station NH 05 off Newport, Oregon, indicates the transition from a southern, warm-water zooplankton assemblage to a northern, cold-water assemblage (Peterson & Keister 2003, Peterson & Schwing 2003, Hooff & Peterson 2006, Peterson et al.

2006). The timing of ocean entry of the tagged smolts in relation to the spring transition was calculated by subtracting the date of the transition from the date of entry into the plume by each group in each year.

Lower river gas saturation (PDG). We obtained gas saturation data, measured as percent dissolved gas (PDG), from an automated US Army Corp of Engineers water quality monitoring station located at Camas, Washington/Washougal, Oregon (CWMW), 40 km downstream of Bonneville Dam (Figure 1.1; www.cbr.washington.edu/dart/). Hourly values were averaged over the period between median arrival date on the acoustic sub-array below Bonneville Dam or release date at Bonneville Dam and the plume entry date for each salmon group in each year.

Sea-surface temperature (SST). SST (°C) is measured hourly at several NOAA data buoys (NDB) off the Columbia River. NDB 46041, located approximately 111 km northwest of the mouth of the Columbia River (Figure 1.1), had a complete SST data set for periods when tagged juvenile salmon were transiting the plume (www.ndbc.noaa.gov/). Hourly values collected at this buoy were averaged over the period between plume entry and plume departure for each salmon group in each year.

River discharge (DIS). River discharge data are recorded at Beaver Army Terminal near Quincy, Oregon, 150 km downstream of Bonneville Dam (Figure 1.1). This is the last discharge recording station in the Columbia River. Daily mean discharge is recorded in cubic feet per second (converted to cubic meters per second) and was extracted from the National Water Information System (http://waterdata.usgs.gov/). Daily values were averaged over the period between plume entry and plume departure for each group in each year.

Turbidity (TB). River turbidity is measured daily at Bonneville Dam in units of Secchi-feet (converted to Secchi-meters), and the data were accessed through Columbia River DART (www.cbr.washington.edu/dart/). Bonneville Dam is located at River Mile 146.1, well upstream of the plume, but it is the closest continuous measurement of turbidity available. Turbidity in the plume should lag turbidity measured at Bonneville, with the lag time dependent on discharge levels. To estimate lag times for each group, we used the difference between their median arrival date at Astoria and median arrival, or release, date at Bonneville. Based on previous studies correlating juvenile travel time and discharge, we believe that using detection data to establish a lag time between turbidity measure and turbid water mass arrival in the plume is reasonable (Berggren & Filardo 1993). Lagged daily turbidity measurements were averaged over the period between plume entry and plume departure for each group.

Analysis

Plume survival and occupancy

Estimates of yearling Chinook salmon (*Oncorhynchus tshawytscha*) survival in the plume were obtained using the data and analytical methods described in Porter et al. (2012b). Briefly, a total of 4646 acoustic tagged smolts were released in the Columbia River basin from 2008 to 2011 (Table 1.1). Detection data from the array components extending from the Snake River to Lippy Point, British Columbia, Canada (Figure 1.1), were used to estimate apparent survival for each treatment group between each detection site in each year using a special case of the Cormack-Jolly-Seber (CJS) live-recapture modeling framework, implemented in the program MARK (Table 1.1; Lebreton et al. 1992, White & Burnham 1999). Unique detection probabilities (p) for each release group were estimated at each sub-array in the river; however, at the ocean sub-arrays, a common p for the groups was used each year. Eight of the 19 fish detected migrating upriver in their release year were detected at the river mouth, but not at Willapa Bay. We did not remove them from the analysis because they affect plume survival estimates by only a fraction of a percent and have no effect on the final results. However, all upstream migration detections were scrubbed prior to analysis.

In 2010 and 2011, an additional sub-array was placed at Sand Island, seaward and adjacent to the Astoria sub-array (Figure 1.1). Porter et al. (2012a) report

2010 and 2011 plume survival in 2 segments: Astoria and Sand Island and Sand Island to Willapa Bay. To permit inter-year comparisons, the methods in Porter et al. (2012a) were modified by setting survival to Sand Island at 1 so that mortality was estimated from Astoria to Willapa Bay. Plume survival estimates in 2008 and 2009 are as reported in Porter et al. (2012a). Median ĉ goodness-of-fit tests, carried out in the program MARK, of the 2008, 2009, and 2011 special-case CJS models used to estimate plume survival did not give evidence of extra-binomial variation (i.e. greater variability than would be expected under binomial sampling, which, if present, would result in underestimates of the variance of the CJS model parameters; Burnham & Anderson 2002). We made corrections to the 2010 survival estimates because there was evidence of minor overdispersion (ĉ = 1.16; Burnham & Anderson 2002).

Plume occupancy included the period between plume entry and plume departure. Entry and departure dates were calculated as the median of final detection dates on the Astoria sub-array (plume entry; Figure 1.1) and the median of final detection dates on the Willapa Bay sub-array (plume departure; Figure 1.1). Plume entry and departure were calculated for each group in each year. Median absolute deviation of the plume entry time (i.e. the spread) was calculated for each group in each year.

Modeling survival and plume residence time

If smolt survival was mediated by travel time through the plume, time-scaled survival, calculated as $S_{TS} = S_P^{\frac{1}{T_P}}$, should be nearly constant and survival could be explained as an exponential decay process, which is time dependent. We fit an exponential decay model to the survival estimates using the nls function in R (R Development Core Team 2011):

$$S_P = e^{-k \cdot T_P}$$

where S_P is plume survival, T_P is median residence time, k is the mortality rate constant, and e^{-k} is the apparent daily survival rate. The assumptions of nonlinear regression—(1) correct function, (2) homoscedasticity, and (3) normally distributed error terms—were evaluated with a plot of the fitted regression curve, a plot of the model residuals against fitted values, and a quantile-quantile (QQ) plot, respectively (Kutner et al. 2005, Ritz & Streibig 2008). We obtained an estimate of the bias in k through bootstrap resampling (n = 10 000; Kutner et al. 2005). We calculated the confidence intervals for the exponential decay model by log transforming the confidence intervals of the linear form of the exponential model,

$$\log S_p = -k * T_p$$

We plotted logit-transformed survival estimates and residuals from the exponential decay model against the variables representing productivity (BST, CU2, CU4) and gas supersaturation (PDG) to evaluate the potential role of biological productivity and exposure to supersaturated river water on plume survival (Kutner et al. 2005). We also calculated the coefficients of determination (R^2) between logit-transformed survival estimates and each of the variables representing productivity and exposure.

We used linear regression models and information theoretic approaches to evaluate the environmental factors potentially governing plume residence time (Burnham & Anderson 2002, Johnson & Omland 2004, Kutner et al. 2005). Our general model of plume residence time, which included 3 covariates and 1 interaction term, was:

$$T_P \sim SST + UP + DIS + UP:DIS$$

We used corrected Akaike information coefficients (AICc), Akaike weights (w_i), and evidence ratios, implemented in R with the package MuMIn, to evaluate and rank the general model and 8 sub-models in our candidate set (Burnham & Anderson 2002, Barto 2012). We used diagnostic plots of the residuals to assess whether the assumptions of linear regression were met for the top ranked model.

Additionally, the residuals of the top model were plotted against variables omitted from the general model to verify that they did not add descriptive or predictive power (Kutner et al. 2005).

Model evaluation with 2006 survival data

Although lower river and plume survival were conflated in 2006 due to the lack of a sub-array at Astoria, we derived estimates of plume survival and residence time for 2006 using travel times and average survival between Bonneville Dam and Astoria from 2008 to 2011. The derived estimates are plotted against the exponential decay model output as an additional test of the model's adequacy. We estimated plume survival in 2006 by dividing the 2006 estimates of combined lower river/plume survival (Bonneville Dam to Willapa Bay) by the average lower river survival (Bonneville Dam to Astoria) in 2008 to 2011 (average = 0.85). We used the range of lower river survival from 2008 to 2011 (0.71 to 0.99; Porter et al. 2012a) to estimate a 2006 maximum and minimum plume survival (Table 1.2). To estimate 2006 plume residence time, we first calculated the average proportion of time spent in the plume relative to the combined time in the lower river and plume for 2008 to 2011 (proportion = 0.64). This proportion was multiplied by the 2006 combined lower river/plume residence time to yield estimates of 2006 plume residence time for each group (Table 1.2).

Table 1.2. Estimates of combined lower river/plume survival and residence time and derived plume residence time and survival for acoustic-tagged Chinook smolts released in 2006 in the Snake River (SR_06) and Columbia (CR_06), or Snake River-sourced smolts that were transported and released below Bonneville Dam (ST_06).

Year	Group	No. of fish	Combined residence time (d)	Combined survival (SE)	Derived plume residence time (d)	Derived plume survival (range)
2006	SR_06	380	3.73	0.71 (.19)	2.40	0.83 (0.72-1.00)
	ST_06	203	8.10	0.56 (.14)	5.22	0.66 (0.56-0.79)
	CR_06	398	5.76	0.81 (.20)	3.71	0.95 (0.82-1.00)

Assumptions and Tests

The use of acoustic telemetry and CJS modeling to estimate survival requires a number of assumptions, including that (1) there are no tag effects, (2) tags are not lost, (3) the size range of fish used in the study is representative of the source populations and there is no effect of fork length on survival, (4) every tagged smolt has the same probability of being detected, (5) sampling is instantaneous, (6) the offshore extent of the marine sub-arrays is sufficient to bound the early marine migratory path, and (7) smolts departing the Columbia River migrate north. Here, we summarize the results of tests of these assumptions, which are also available in uncondensed form in Porter et al. (2009b, 2010, 2011, 2012a,b).

Captive tag effects and tagging-induced mortality studies were conducted in 2008 to 2011 to study the survival, tag retention, and growth of *Oncorhynchus tshawytscha* smolts implanted with V7-2L dummy acoustic tags (DATs) relative to PIT-tagged controls (Porter et al. 2009b, 2010, 2011, 2012b). Small initial effects on growth rates of DAT tagged smolts were observed. Tag retention was high; no V7-2L DATs were shed in 2008. In 2009, 9 (of 210) DATs were shed, 2 (of 188)

were shed in 2010, and 1 (of 87) was shed in 2011. In all years, there were no significant differences in survival or mean fork length between the DAT-tagged and control fish at the conclusion of the studies. To ensure that tag burdens were unlikely to impact survival, we restricted tagging in all years to smolts with a minimum fork length (FL) of 130 mm (one 129 mm smolt was tagged in 2008), which is below the ratio of tag size to smolt size where tag burdens have been found to be significant (Lacroix et al. 2004). Ninety-two percent of tagged smolts also had tag burdens <6.7% of their body weight, the level at which Brown et al. (2006) found that tag burdens may begin to exert an effect on survival.

The 130 mm FL minimum generally restricted tagging to the upper 68 to 88% of the study populations. In 2008, Snake River smolts collected at the Dworshak hatchery were small, and tagged smolts represented only the upper 10% of the population of smolts reared at Dworshak National Fish Hatchery. However, the fork length spectrum represented 76% of the population of hatchery Chinook sampled at the Lower Granite Dam smolt monitoring facility in 2008. Fork length ranges and the proportions of study populations they represent are reported in Table 1.1. Smolt size has been linked to adult returns and may influence early marine survival (Tomaro et al. 2012). We recorded fork lengths at tagging and compared the fork length frequency distributions of the released fish to those that survived to Willapa Bay. If larger size conferred a survival advantage to Willapa Bay, we would expect the size distribution of survivors to be right skewed relative to the overall release group. However, the distributions were virtually identical,

indicating that there was no size-selective effect (Figure 1.2).

Violations of the assumption that every tagged smolt has the same probability of detection should be evident in a lack of fit of standard CJS models to the detection data (the standard CJS model has unique parameters for the probability of survival to, and detection at, each sub-array and thus contains more parameters than the special-case model used to estimate survival in this analysis). There was no evidence in median ĉ tests, conducted in the program MARK, of a lack of fit to the 2008 through 2011 data, indicating that this assumption was not violated (Porter et al. 2012a). Instantaneous sampling is the assumption of demographic closure at each sampling period, and, in practice, sampling periods in mark-recapture studies are short, rather than truly instantaneous. From 2008 to 2011, individual fish crossed the arrays within hours of first detection, and the sampling periods at the lower river and Willapa Bay sub-arrays (i.e. the periods between arrival of the first and last smolts in each

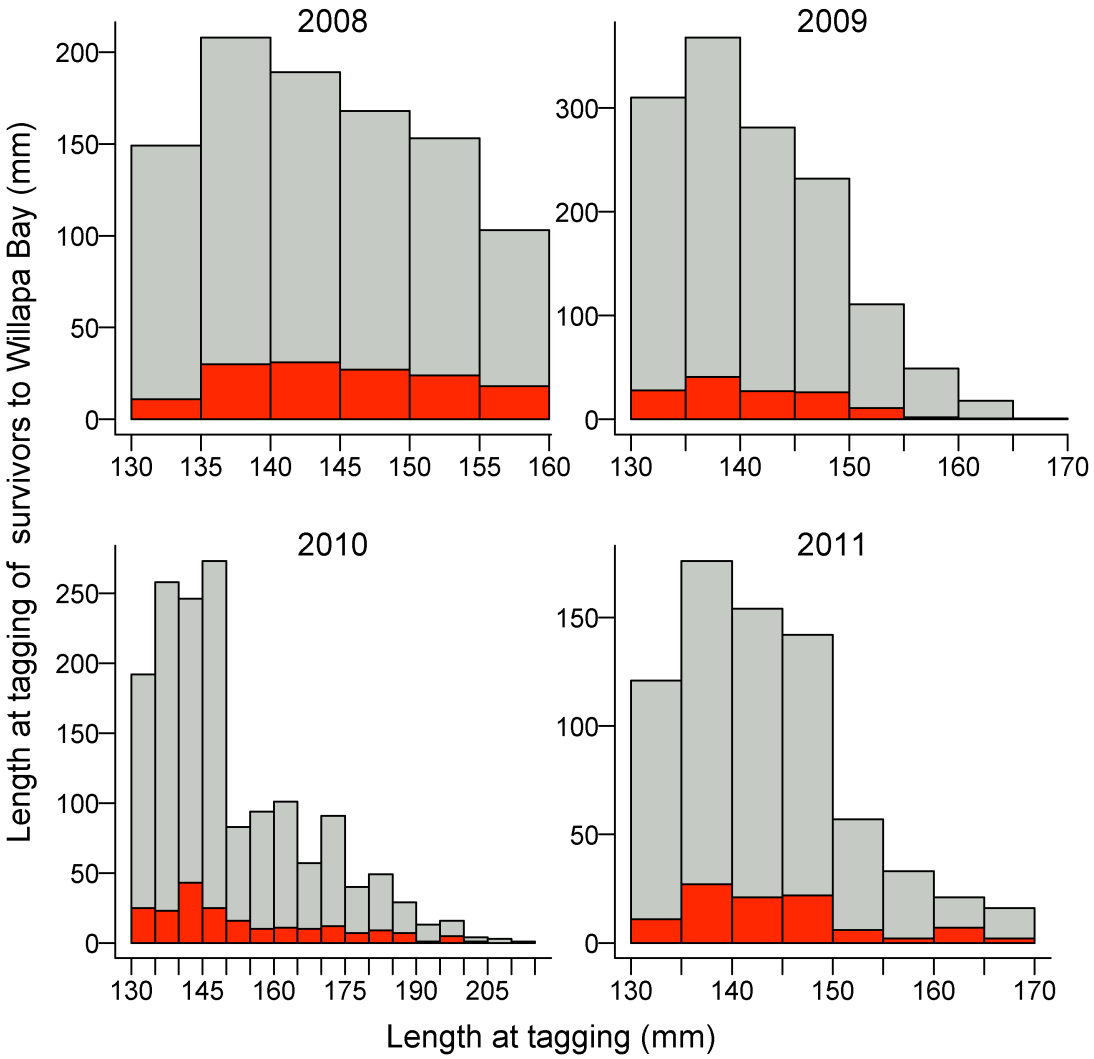

Figure 1.2. Frequency distributions of the fork lengths of all tagged smolts (gray) and smolts detected at the Willapa Bay sub-array (red). Fork length was measured at the time of tagging. The similarity in the distributions indicates that there was no size-selective effect on survival to the Willapa Bay sub-array.

group) only lasted for several days.

Extensive ocean sampling of juvenile salmon off Oregon and Washington has shown that juveniles are generally confined to the shelf region (Bi et al. 2007, Peterson et al. 2010). From 2008 to 2010, the sub-array at Willapa Bay extended offshore to the 200 m isobath, but was extended to the 500 m isobaths in 2011 because smolts continued to be detected on the outermost receivers. In 2011, 9 smolts were detected on the extended receivers, indicating a small number of smolts may have passed outside the detection range of the Willapa Bay sub-array in 2008 to 2010. No smolts were detected on the outermost receivers in 2011, although the receivers were lost, likely to fishing activity, sometime during the 2011 migration season (Porter et al. 2012a). Missed detections could result in a downward bias in plume survival estimates, although CJS modeling alleviates this problem by using subsequent detections at the Lippy Point sub-array (which are heavily skewed towards the inner shelf) to adjust estimates of survival at Willapa Bay (Porter et al. 2012a).

Miller et al. (1983) demonstrated with north- and south-opening nets that juvenile salmon swim north after entering the ocean. In 2009 and 2011, a sub-array was deployed at Cascade Head, Oregon, to verify the assumption that fish swim north at ocean entry (Figure 1.1). The small number of detections at Cascade Head (3 fish in 2009 [number released = 1370] and 6 in 2011 [number released = 725]),

suggest the conclusion by Miller et al. (1983) was correct. One of the 6 tagged fish detected at Cascade Head in 2011 was subsequently detected at both Willapa Bay and Lippy Point, further supporting this conclusion. Fish detections at Cascade Head were included in the Willapa sub-array detections to reflect their survival in the plume. We have excluded a group of transport fish released in early-April 2009. This group was released much earlier in the season than the remaining groups (Porter et al. 2009b) and may have entered the plume before predators became abundant (see 'Discussion').

Results

Initial exploration with pairwise plots of the variables and their Pearson correlation coefficients revealed that several variables potentially related to survival, but without clear mechanistic relationships, were also associated with plume residence time. Thus, we divided the variables into 2 categories, those that might affect survival of *Oncorhynchus tshawytscha* indirectly by influencing plume residence time (upwelling at ocean entry, discharge, SST), and those that might directly affect survival by way of feeding opportunities (timing of the biological spring transition, 2 and 4 wk cumulative upwelling prior to ocean entry) or reduced physiological fitness (dissolved gas levels). We excluded turbidity (measured at Bonneville Dam) due to its high correlation with discharge (Pearson correlation coefficient = 0.95) and the distance (146 km) between the dam and the plume. Similarly, we did not consider spill at Bonneville Dam (the final dam in

the river) because it is correlated with discharge and does not reflect additional downstream freshwater inputs to the plume.

Plume survival varied widely, but the daily plume survival rate (S_{TS}) was similar among groups (Figure 1.3). The estimated mortality rate constant, k, across the groups was 0.12 d^{-1}. There was no evidence of violation of homoscedasticity in the exponential decay model, the error terms appeared normal, and the bias of the estimate of k was low (bias = -0.003). However, the plot of the fitted regression curve suggests that the model performed well in predicting survival of the groups that migrate in-river, but did not perform as well for groups transported and released below Bonneville Dam (Figure 1.4). In-river migrants entered the plume in a more continuous fashion, whereas transported fish entered in brief pulses; the median absolute deviation from the median plume entry date of transported juveniles was < 1 d (mean = 0.56 d), but ranged from 1 to 7 d (mean = 3.39 d) for the in-river migrants (Figure 1.4). The plume residence time of all groups was brief, averaging 7.29 d (Table 1.3).

The high variability in survival of the 2008 to 2011 transport groups limits further inference regarding these groups, and the remaining results pertain only to the in-river groups (transport group data are plotted in Figure 1.5 for reference). Plots of logit-transformed survival estimates against timing of the biological spring transition relative to plume entry and 2 and 4 wk cumulative upwelling prior to

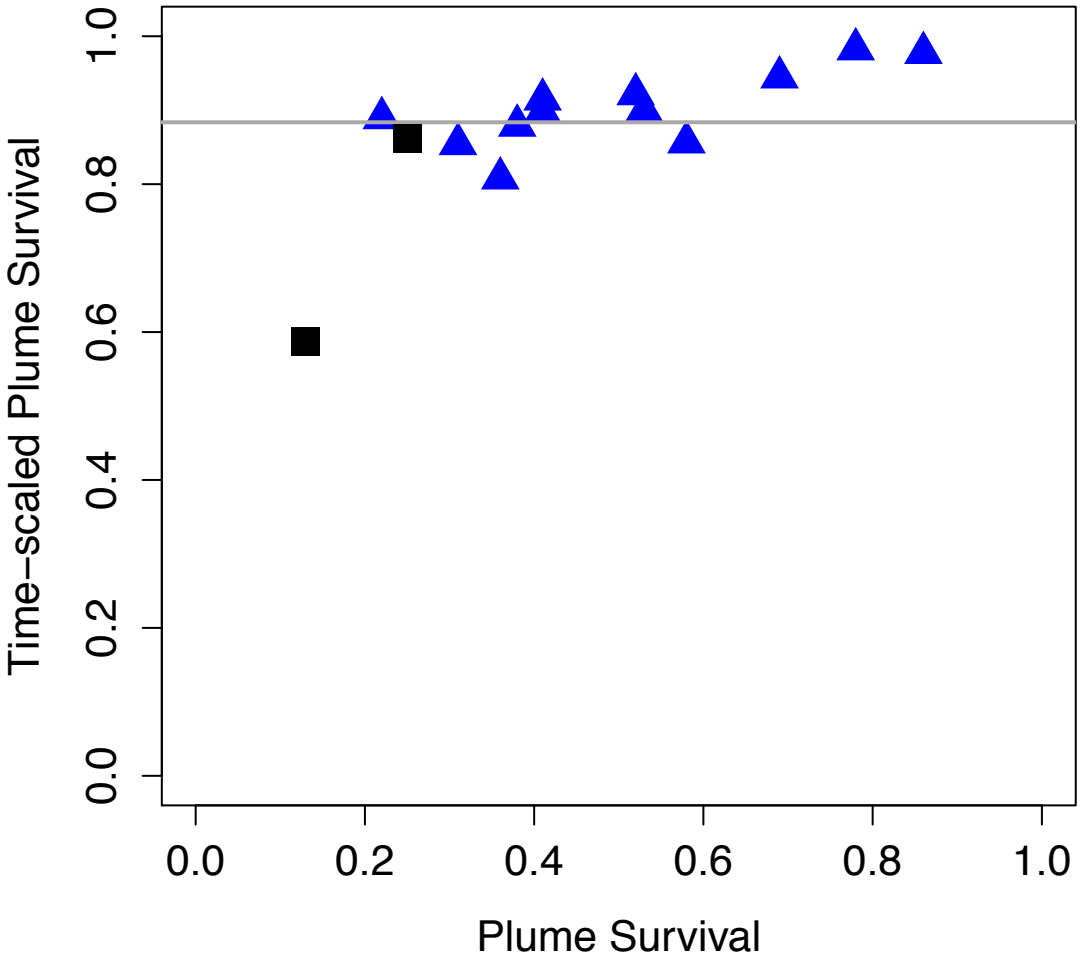

Figure 1.3. Comparison of plume survival with daily survival rates (squares and triangles). Although plume survival varied widely, the daily survival rate was similar among groups, illustrating the potential effect of residence time on plume survival. The outlier with both low survival and low time-scaled survival was 1 of 2 groups (squares) exposed to high total dissolved gas concentrations (TDG > 120%) in the lower river. The gray line is the model estimated daily survival rate.

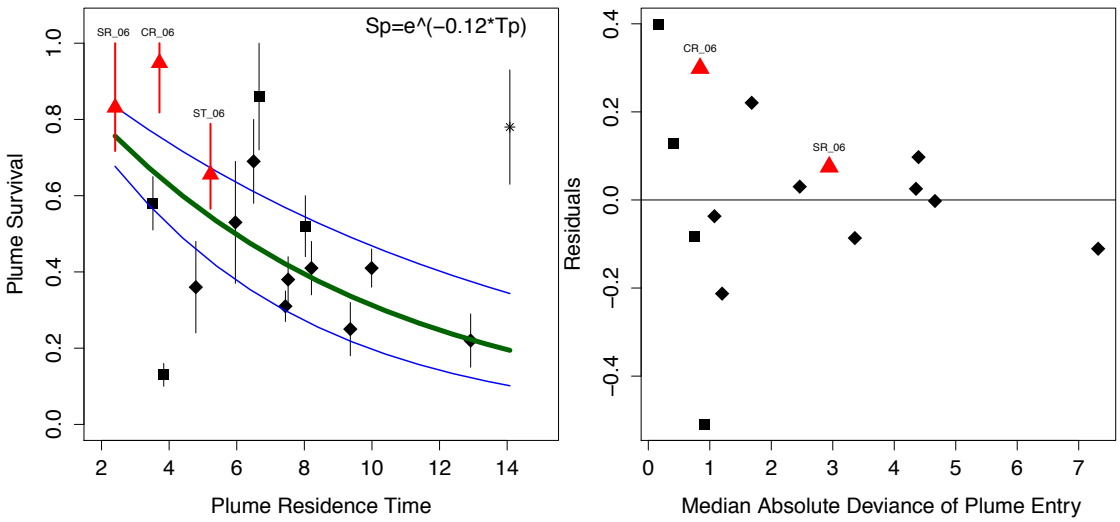

Figure 1.4. (a) Comparison of plume survival with plume residence time, showing the regression curve (thick green line) and 95% confidence intervals (thin blue lines). The model clearly fits the in-river migrant groups (diamonds, ±95% CI) better than transported groups (squares, ±95% CI). Derived estimates of 2006 plume survival and residence time (red triangles; vertical red lines show maximum and minimum estimates) also fit the pattern of a simple exponential decline in survival with residence time. The 2009 early-release transport group exclude in calculations is also shown (star , ±95% CI). (b) Residuals from the regression relationship exhibit greater variance when the spread in plume entry time is low (measured by absolute deviation), as is also the case for all of the transport groups (squares) in this study. Median absolute deviation at the Bonneville dam sub-array is shown for 2006 (triangles); there are no data for the 2006 transport group as they were released in the vicinity of the Bonneville sub-array.

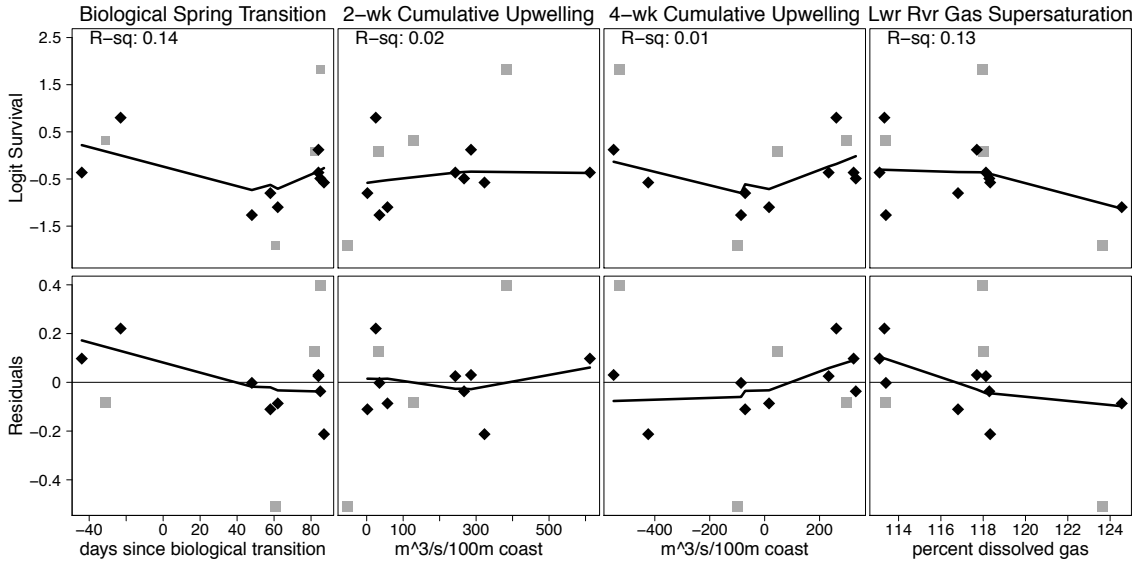

Figure 1.5. Upper panels: logit-transformed survival compared with measures of coastal productivity and lower river total dissolved gas levels; no clear relationships are evident. Lower panels: plots of residuals from the exponential decay model do not reveal patterns indicating that the model would be improved by including biological productivity or exposure to gas supersaturated water. Coefficients of determination (R^2) and Friedmans's supersmoother lines (R Development Core Team 2011) are fitted to the in-river groups (diamonds). Transport group data (squares) are shown for reference.

Table 1.3. Plume residence time and environmental data summary. The ST_09ER group, shown for reference, was not included in the analysis. For explanation of the group designations, see Table 1.1.

Group	Plume residence time (d)	Days since biological spring transition	Cumulative upwelling (m^3 s^{-1} 100 m^{-1})		Percent dissolved gas	Sea-surface temperature (C°)	Upwelling (m^3 s^{-1} 100 m^{-1})	Discharge (m^3 s^{-1})
			2 wk	4 wk				
SR_08	8.21	84	243	233	118.1	11.46	8.22	13756.4
ST_08	8.03	82	32	48	118.0	11.42	12.44	13866.7
CR_08	7.52	85	267	332	118.3	11.44	10.44	13496.3
SR_09	5.96	84	286	-550	117.7	13.16	9.71	11194.7
ST_09	6.66	85	383	-527	117.9	13.49	3.57	11271.6
ST_09ER	14.1	51	470	445	113.3	9.95	-27.87	9551.8
CR_09	4.79	87	323	-424	118.3	13.82	2.80	11243.3
SR_10	6.50	-23	25	261	113.3	13.43	18.50	12461.1
ST_10	3.52	-31	128	297	113.4	11.02	14.00	8814.2
CR_10	9.99	-44	612	324	113.1	11.00	-34.55	8074.7
SR_11	9.36	62	57	16	124.6	12.33	2.00	16717.2
ST_11	3.84	61	-52	-98	123.7	11.49	-7.20	16419.6
UC_11	7.44	58	2	-71	116.8	11.47	1.75	14940.6
MC_11	12.9	48	35	-86	113.4	10.73	6.79	13781.0

plume entry did not provide evidence of any influence on plume survival (Figure 1.5). Additionally, there were no strong patterns in the plots of the model residuals against these variables to suggest that incorporating them would improve the model (Figure 1.5).

Survival appears lower at higher (>120%) levels of dissolved gas supersaturation, which may be evidence of a threshold level of exposure at which gas supersaturation levels experienced in the lower river noticeably affect subsequent plume survival, although the evidence for this is weak (Figure 1.5). The density of data points at high levels of dissolved gas is less than at lower levels, and the apparent relationship is determined by low survival in a single year, 2011, when dissolved gas levels below Bonneville Dam exceeded the 120% limit established under Oregon and Washington water quality law (USACOE 2011). We did not

see evidence in the residual plot that this exposure should have been incorporated into the survival model (but see 'Discussion').

In 2006, smolt travel time between Bonneville Dam and Willapa Bay was short and survival was high, as are the derived estimates of plume residence time and survival (Table 1.2; Porter et al. 2012a). Additionally, the model performs better in predicting survival of the SR_06 group, which entered the lower river in a more continuous manner than the CR_06 group (Figure 1.4). Refitting the exponential decay model to include the 2006 data only changes the decay constant slightly, from 0.12 to 0.11.

Among the 9 candidate models for predicting plume residence time, the model containing only SST outperformed all others, as measured by AICc distance and model weights (weight = 92%; Table 1.4 and Figure 1.6). Diagnostic plots of the SST model did not show evidence of heteroscedasticity or non-normal error terms, and there were no patterns in the plots of the SST-model residuals against the omitted variables, upwelling and discharge, to indicate that that these variables should be included.

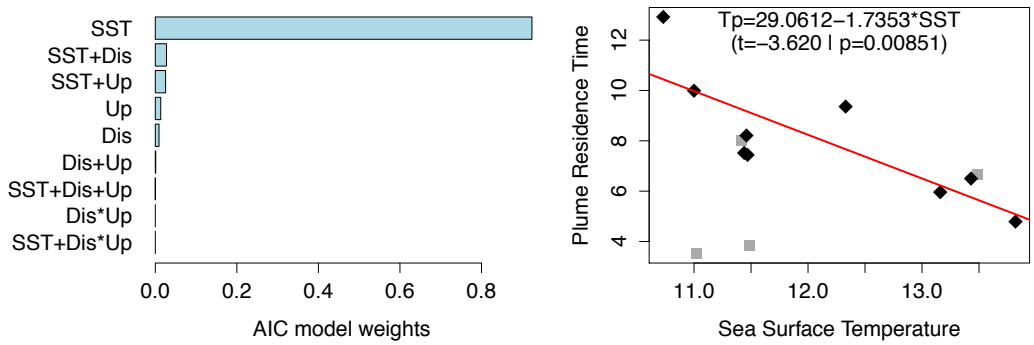

Figure 1.6. (a) Model ranking for the influence of environmental variables on plume survival; the sea-surface temperature (SST) model receives the greatest proportion of model weight. (b) The inverse relationship between SST and plume residence time suggests that most of the predictive power occurs because smolts do not remain in the plume for long when coastal temperatures are high, increasing survival to Willapa Bay. Diamonds: in-river migrants; squares: transport groups. For explanation of model abbreviations, see Table 4.

Table 1.4. AIC-based ranking of 9 candidate models of plume residence time containing hypothesized combinations of 3 predictor variables, sea-surface temperature (SST), upwelling (UP), and river discharge (DIS). Evidence is a measure of how many times less likely the model is the best model relative to the top ranked model. AICc: corrected Akaike's information criterion.

Model	Parameters					AICc	ΔAICc	Model Weight	Evidence
	Intercept	SST	Upwelling	Discharge	Disch:Up				
SST	29.06	-1.74	-	-	-	41.77	0	.92	1.0
SST+Dis	27.83	-1.72	-	0.000078	-	48.81	7.034	.027	33.7
SST+Up	29.12	-1.74	0.00094	-	-	48.97	7.19	.025	36.6
Up	8.228	-	-0.053	-	-	50. 25	8.47	.013	69.2
Dis	5.966	-	-	0.00016	-	51.0092	9.24	.0091	101.3
Up+Dis	1.838	-	-0.10	0.00051	-	55.37	13.59	.0010	894.6
SST+Up+Dis	25.89	-1.62	-0.016	0.00014	-	60.69	18.92	.000071	12834.7
Up*Dis	-2.11	-	-0.66	0.00069	0.000058	65.056	23.28	.0000081	113745.3
SST+Up*Dis	22.15	-1.45	-0.20	0.00023	0.000018	84.37	42.59	.0000000052	1778441824.7

Discussion

The Columbia River plume was once posited to benefit juvenile salmon by providing food and refuge while transporting them to safer environs (Casillas 1999). However, research has shown that juvenile salmon do not take advantage of feeding opportunities presented by the plume (DeRobertis et al. 2005, Morgan et al. 2005) and that the plume is rich in salmon predators (Collis et al. 2002, Anderson et al. 2004, Lyons et al. 2005 Emmett et al. 2006). More recently, acoustic telemetry studies have shown that yearling Chinook (*Oncorhynchus tshawytscha*) survival in the plume is low in relation to river, estuary, and coastal ocean habitats (Porter et al. 2010, 2012a). Thus, the telemetry data suggest that reducing plume residency may increase yearling Chinook salmon productivity by allowing the smolts to move into regions with higher survival, which runs contrary to initial thinking that the plume might be a refuge where longer residence could increase adult return rates.

Although plume survival estimates in this study ranged from 0.13 to 0.86, they stabilized when scaled by residence time (Figure 1.3). If mortality rates in the plume are consistent at comparable periods in the migratory season (groups used in this analysis were released at similar periods each year), then plume survival could be governed by residence time. Consistent with this idea, we find that a simple exponential decay model largely describes plume survival, although the model performs best when analysis is restricted to groups of yearling Chinook whose individuals enter the plume over a longer time period. This scenario is also consistent with the hypothesis that predation is a key driver of survival in the plume region and provides a plausible bridge between survival and environmental variables, such as river discharge and SST, that have been hypothesized to influence early marine survival, but lack a clear link. The derived estimates of 2006 plume residence time and survival provide additional qualitative support to the idea that plume survival is negatively related to travel time.

The variability in plume survival of the 2008 to 2011 transport groups relative to the fitted regression line suggests that there may be substantial variation in mortality events around the average daily rate that we propose. Over short periods of time (< 1 d), pulses of smolts travelling between the Astoria and Willapa Bay sub-arrays may or may not encounter significant numbers of foraging predators, resulting in groups experiencing either very high survival if they pass through the plume without encountering predator aggregations, or very

low survival if they encounter substantial number of predator groups. In this scenario, survival of such groups would appear to be more variable than groups whose plume entry times are more dispersed over time, even though the same underlying mortality rate process may apply.

We believe that plume residence times (average: 7.29 d) were too short for starvation to have had an effect and that predation was the most likely cause of plume mortality. The density of piscivorous hake (*Merluccius productus*) in the plume generally increases in May and peaks in June and July (Agostini et al. 2006, Emmett et al. 2006), and, similarly, the contribution of salmonids to the diet of Caspian terns (*Sterna caspia*) and double-crested cormorants (*Phalacrocorax auritus*) that nest near the plume peaks in May (Collis et al. 2002, Lyons et al. 2005). Predation by these piscivorous birds and fish may exert significant top-down control on plume survival (Collis et al. 2002, Anderson et al. 2004, Lyons et al. 2005, Emmett et al. 2006, Emmett & Sampson 2007), although this has not been conclusively demonstrated. We suspect that the high survival of the early-April 2009 release group, despite a long plume residence time, may be related to the May and June peaks in predation by piscivorous birds and fish (Collis et al. 2002, Anderson et al. 2004, Lyons et al. 2005, Emmett et al. 2006). This is consistent with an effect of emigration timing on early-marine survival (Muir et al. 2006) and the idea that the mortality rate may vary through the migration season. Unfortunately, with only a single data point and no predator data, any inference is severely restricted.

Although the temporal match, or mismatch, between juvenile salmon entering the plume and the timing of spring increases in marine productivity and advection of lipid-rich copepods into marine waters off Oregon and Washington (the biological spring transition) may affect feeding opportunities, plume survival of the groups used in this study does not appear to be related to biological productivity measures. However, biological productivity and the availability of higher quality prey is still potentially relevant to survival at larger temporal scales as it may affect whether juveniles obtain sufficient energy reserves to survive their first winter at sea (Beamish & Mahnken 2001, Tomaro et al. 2012).

The practice of spilling water over Columbia River dam faces (rather than through turbines) to reduce the physical and physiological stress on juvenile salmon can supersaturate the river below the dam with atmospheric gases, potentially leading to gas bubble trauma and, when exposure is non-lethal, reducing fitness (Bouck 1980, Mesa & Warren 1997). During the 2008 to 2011 period, percent dissolved gas levels recorded at the Camas/Washougal monitoring station below Bonneville Dam ranged from a relatively benign 113% to a potentially harmful 125% during flood conditions in 2011 (Bouck 1980, USACOE 2011). Although we found little evidence that dissolved gas exposure explains the variation in plume survival among the groups used in this analysis, an intra-year analysis of the smolts released in 2011 after total dissolved gas levels exceeded state regulatory

limits at the Bonneville Dam release site suggests they may have experienced lower daily survival rates in the river and plume compared with their unexposed counterparts (I. G. Brosnan et al. unpubl. data).

Plume residence time may be affected by water temperature, which has been related to migration timing and speed (Brett et al. 1958, Sykes & Shrimpton 2010, Martin et al. 2012), and river discharge and wind-driven surface currents (reflected in the coastal upwelling index) that may affect travel time by changing the area and depth of the plume and adjusting its orientation between a northern, onshore configuration, or a southwestern, offshore configuration (Hickey et al. 2005, Burla et al. 2010b). The best model of plume residence, by a significant margin, included only SST. Models that included river discharge, which can be influenced by management action, or coastal upwelling, have little weight. This is consistent with Burla et al. (2010a), who found that the physical dynamics of the plume at the time of ocean entry do not affect adult returns of yearling Chinook (although it may affect steelhead salmon returns). If our results are widely applicable, they also suggest that plume survival may not be amenable to improvement via management of the hydropower system, although it is conceivable that hatchery and fish transport releases could be timed to minimize plume residence. However, this would require detailed forecasts of conditions in the early marine environment that are not presently available.

Advances in marine acoustic telemetry have played an important role in addressing scientific questions and conservation problems in the Columbia River basin. Rechisky et al. (2009, 2012, 2013, 2014, this volume) and Welch et al. (2009, 2011) have measured directly the survival of juvenile salmon in key marine habitats and conducted direct experimental tests of survival hypotheses related to dam passage and the downriver transport of juvenile Chinook. Additional releases of telemetered yearling Chinook would provide greater clarity regarding the drivers of plume residence time and could better address the question of plume survival in relation to predator abundance and distribution. Nonetheless, we have shown here that a simple exponential decay model adequately described the survival of juvenile yearling Chinook in the Columbia River plume, and that the ability of resource managers to affect plume survival of yearling Chinook by altering residence time may be limited. If correct, this poses a potential problem, as survival in the plume is low relative to other habitats (Porter et al. 2010, 2012a). Survival might potentially be improved by the successful development of marine environmental forecasts to aid in release timing, and the telemetry data used in this analysis can be extended to a value-of-information analysis to determine what the maximum financial outlay should be for such forecasts (Raiffa & Schlaifer 1961, Williams et al. 2011).

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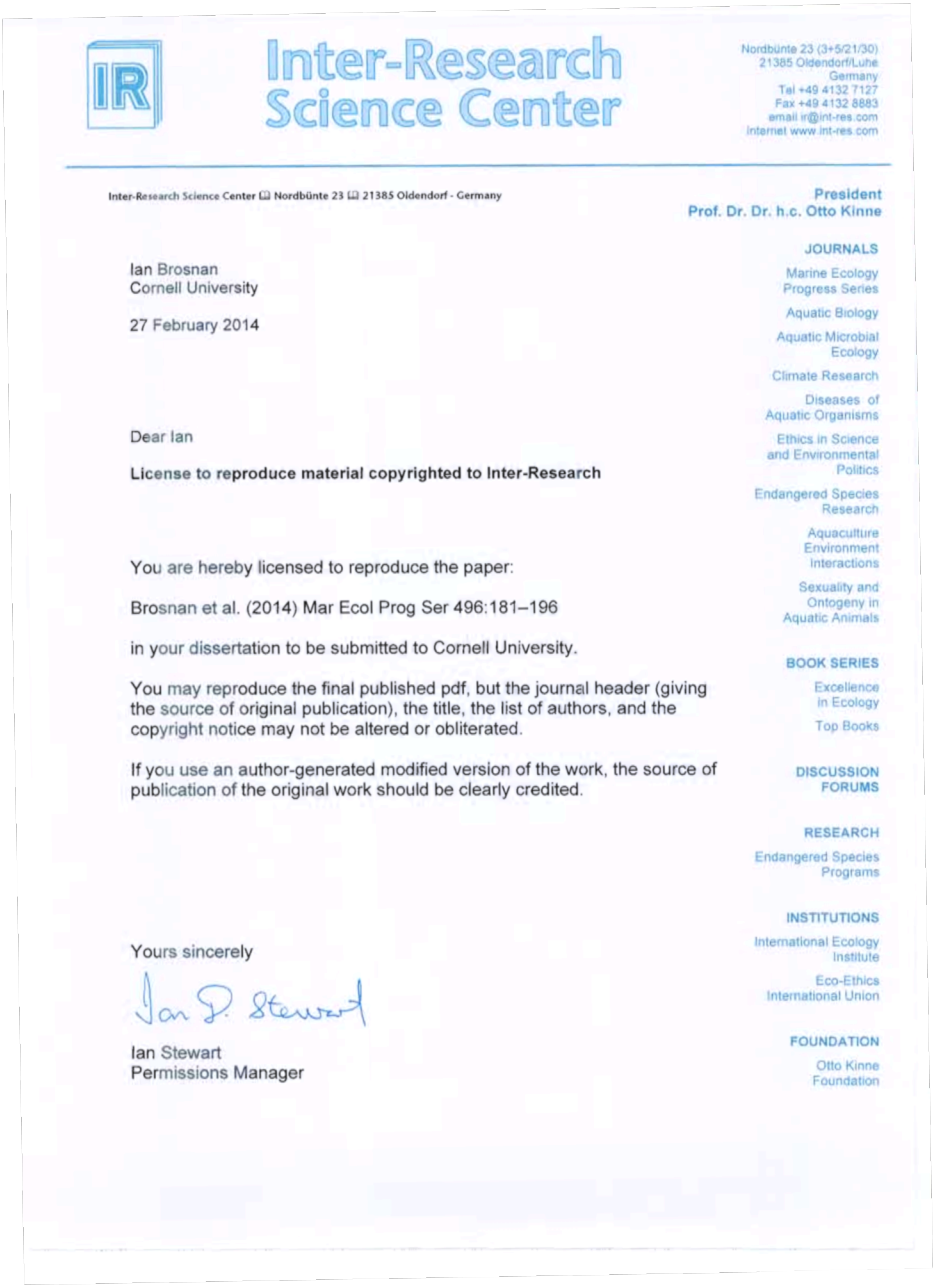

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CHAPTER 2

EFFECT OF GAS SUPERSATURATED WATER ON SURVIVAL OF OUT-MIGRATING YEARLING CHINOOK SALMON IN THE LOWER COLUMBIA RIVER AND PLUME: A RETROSPECTIVE COHORT STUDY

Abstract

Unusually high flows in the Columbia River raised total dissolved gas (TDG) levels in 2011 well beyond the 120% regulatory limit imposed to prevent harmful impacts to aquatic organisms. In-river (IR) migrating juvenile yearling Chinook released at Bonneville Dam with acoustic tags during periods when TDG exceeded 120% received estimated maximum exposures of 134% TDG and subsequent daily survival rates in the lower river were reduced by 0.06 d^{-1} (SE = 0.02) relative to IR migrant fish released when TDG < 120%. Transported smolts (T) released 10-13 km below Bonneville Dam had lower maximum exposure levels (126%) and experienced no difference in daily survival rates relative to unexposed smolts. The same groups of exposed IR and T fish had daily plume survival rates reduced by 0.15 d^{-1} (SE = 0.03) and 0.18 d^{-1} (SE = 0.06) relative to unexposed smolts, possibly due to chronic effects of high TDG exposure. This is the first study to directly assess the potential longer-term influences of gas supersaturation on salmon smolts during the early marine life history period. A controlled study of acute and chronic effects on survival in free-ranging smolts is

warranted given the importance of determining deleterious levels of TDG to salmon conservation and hydrosystem operations.

Introduction

The practice of spilling water over dams in the Federal Columbia River Power System (FCRPS) can induce gas bubble trauma (GBT) in salmon smolts by increasing total dissolved gas levels (TDG) in the river below the spillways. However, passing through the spillway alleviates the physical effects of powerhouse passage and may contribute to improved salmon survival, an issue of particular concern for salmon listed as 'Threatened' or 'Endangered' under the U.S.A. Endangered Species Act (Budy et al. 2002, Petrosky & Schaller 2010, USOFR 2012). Thus, to support fish passage, the states of Oregon and Washington have modified water quality standards to permit elevated TDG levels in dam forebays (115%) and tailraces (120%) during smolt outmigration (USEPA 1986, OCR 2003, OSA 2003, OR 2009).

There is a rich body of literature evaluating the physical, biological, and ecological effects of dissolved gas on smolts (reviews by Weitkamp & Katz 1980 and McGrath et al. 2006), but there have been few studies of either long-term (chronic) effects or direct measurements of survival in the wild following exposure to elevated TDG. The 2013 Draft Supplemental Biological Opinion (Bi-Op) for the FCRPS raises concerns about potential total dissolved gas effects on smolts that would result from a proposed large-scale operational test of the effect of dam spill on smolt-to-adult returns and identifies 2011 as a potentially instructive year for evaluating TDG effects (NMFS 2013).

2011 is instructive because unusually high river flows exceeded the capacity of the powerhouses at Bonneville Dam, resulting in high levels of involuntary[1] spill (USACOE 2011). By mid-May, total dissolved gas levels recorded at the first two monitoring sites below Bonneville Dam exceeded 120%. This event occurred coincident with the release of acoustic tagged juvenile yearling Chinook salmon (*Oncorhynchus tshawytscha)* as part of a study to estimate survival in the lower river and estuary (Bonneville to Astoria, henceforth 'lower river') and the plume (Astoria to Willapa Bay; Figure 2.2). The timing of the releases covered the period before and after dissolved gas levels climbed above state TDG limits, providing an opportunity to compare the effect of exposure to supersaturated water in the lower river on subsequent survival. Here, we evaluate the effect by classifying smolts that were tagged and released below Bonneville Dam after total dissolved gas reached or exceeded the 120% standard as "exposed" and comparing their survival with smolts tagged and released before TDG levels reached this level.

[1] Involuntary spill is distinguished from the voluntary spill at Bonneville Dam that begins annually on April 10th to aid fish passage (USACOE 2011).

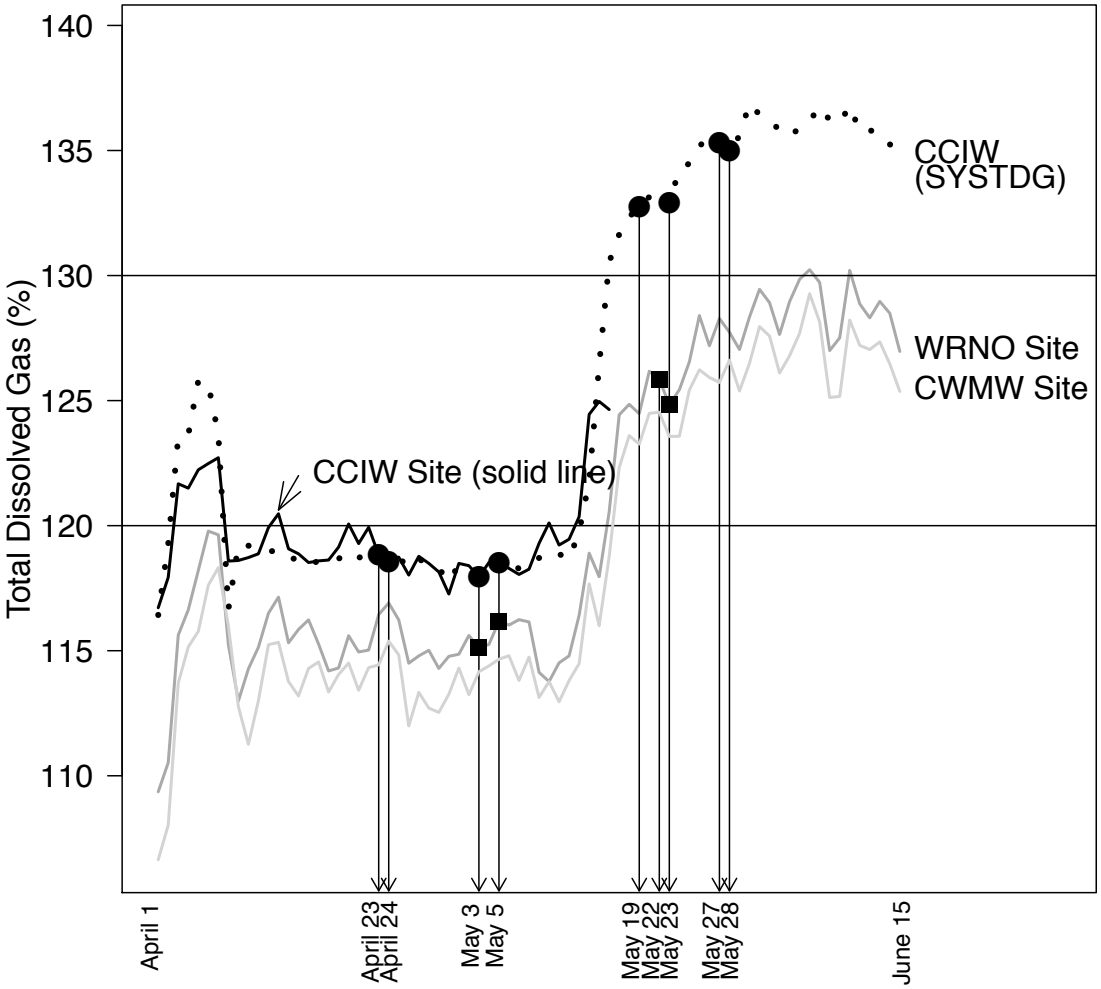

Figure 2.1. Average daily total dissolved gas (%) below Bonneville Dam, calculated using the Oregon methodology from data recorded at three downstream monitoring stations from April 1st through June 15th, 2011. CCIW = Cascade Island site, WRNO = Warrendale site, and CWMW = Camas/Washougal site. Solid lines denote measured values at each station. The dotted line is the prediction for Cascade Island from the SYSTDG model. Horizontal lines mark the 120% TDG limit for dam tailraces and the 130% TDG level referenced in the discussion; arrows mark the release dates for in-river (circles) and transport (squares) groups.

Materials and Methods

Tagging and tracking of yearling Chinook salmon.

Seven-hundred and eighty juvenile yearling Chinook salmon were surgically implanted with VEMCO V7-2L transmitters[2] (7 x 20 mm, 1.6 g in air) and released in the lower Columbia River (Porter et al. 2012; Figure 2.2). Tags were programmed such that the time between successive transmissions was random and uniformly distributed with minimum, maximum and mean transmission intervals of 15, 45, and 30 seconds. The general population of yearling Chinook contributing to this study included hatchery-origin yearling Chinook smolts collected at Lower Granite Dam and hatchery and wild smolts collected at Bonneville Dam. Smolt sizes ranged from 130-170mm and tag burden by weight ranged from 2.7 to 7.9% of body weight. Smolts were accepted for tagging after being examined to confirm minimal scale loss and the absence of external marks or lesions.

Five-hundred and eighty in-river (IR) migrant yearling Chinook smolts were collected at Bonneville Dam and tagged and released at the smolt monitoring facility located below the dam (Columbia rkm 234), approximately one km from the spillway TDG monitoring site at Cascade Island. Smolts were held in tanks

[2] Surgical protocols, tag effects, tag retention, and tag lifespan are briefly reviewed in Appendix A.

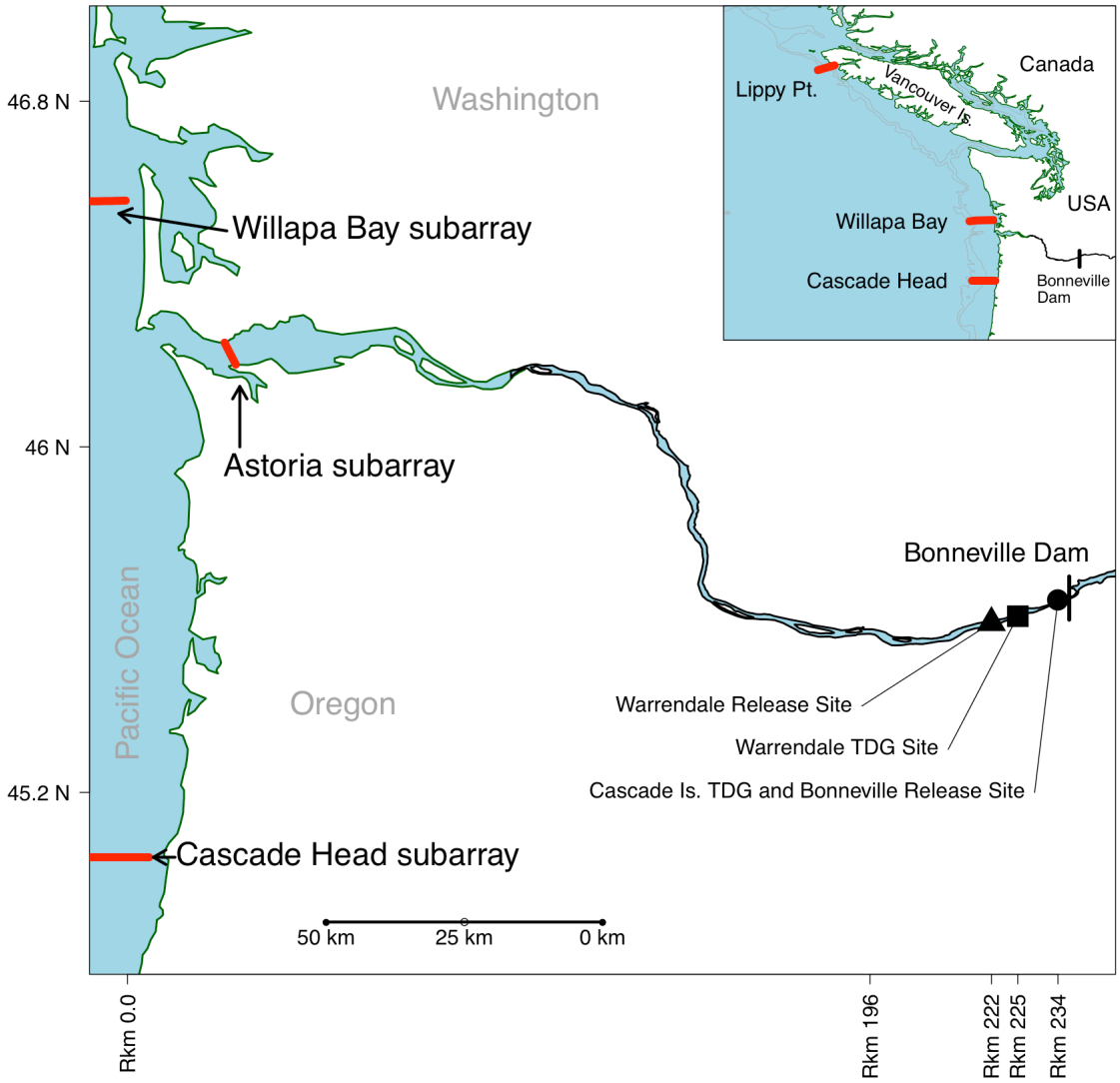

Figure 2.2. Columbia River total dissolved gas monitoring sites below Bonneville Dam, tagged fish release sites, and the sub-arrays of acoustic receivers discussed in the text. The plume region encompasses the area between the Astoria and Willapa Bay sub-arrays.

approximately one meter deep flushed with flow-through river water drawn at the dam forebay. IR smolts were tagged on the day of capture or the next day, and released on the fourth day. Releases occurred in small groups between April 23rd and May 28th. Source stocks for IR tagged smolts were determined using genetic stock identification (GSI; details in Rechisky et al. 2014) An additional 200 juvenile yearling Chinook salmon were collected at Lower Granite Dam in the Snake River for transport (T) and release below Bonneville Dam. They were tagged at the smolt monitoring facility the day after collection, transported by barge downstream on day three, and released four days after collection 10-13 km below Bonneville Dam (Columbia rkm 222-225; Figure 2.2), near the Warrendale TDG monitoring site. Half of the transported smolts were released in early-May and half in mid-May and so are grouped into two transport groups of 100 smolts each (Table 2.1).

Table 2.1. Groups, tagging and release sites, release dates, and numbers of fish tagged in 2011. CCIW = Cascade Island, WRNO = Warrendale, CWMW = Camas/Washougal, SYSTG = SYSTDG model output.

Tagging site (release site)	Group	Treatment	Release dates	No. released	Total Dissolved Gas % at release (source)
Lower Granite Dam (Columbia Rkm 111-115)	Transport	Unexposed	3 May 5 May	47 53	115.1 (WRNO) 116.1 (WRNO)
		Exposed	21 May 22 May	50 50	125.8 (WRNO) 124.8 (WRNO)
Bonneville Dam (Bonneville Dam)	In-river	Unexposed	23 April 24 April	100 100	118.8 (CCIW) 118.5 (CCIW)
			3 May 5 May	50 50	118.0 (CCIW) 118.5 (CCIW)
		Exposed	19 May 22 May	48 101	131.0 (SYSTDG) 131.3 (SYSTDG)
			27 May 28 May	72 59	133.8 (SYSTDG) 133.3 (SYSTDG)

Tagged smolts were tracked downriver and then north in the coastal ocean to Lippy Point, British Columbia, with listening lines ("subarrays") of acoustic receivers that monitored the river mouth at Astoria Bridge and Sand Island, and the continental shelf from nearshore out to the 500m isobath at Willapa Bay, WA, and Lippy Point, British Columbia (Figure 2.2). Lower river and plume survival of the in-river migrant stocks was similar in 2011 (Porter et al. 2012, Rechisky et al. 2014) and there was no a priori reason to suspect that different stocks would exhibit a differential response to TDG exposure, so we did not analyze the data for differences in stock-specific survival.

Estimating lower river and plume survival.

Tagged smolts were classified as exposed or unexposed in the two release categories, IR and T, based on dissolved gas levels recorded at gas monitoring sites proximate to their release locations (Figure 2.2). In-river fish were classified as exposed if they were released after daily total dissolved gas levels reached, and remained above, 120% TDG (the Oregon and Washington tailrace water quality standard) at the Cascade Island monitoring site and unexposed otherwise (Figures 2.1 and 2.2). Transported fish were classified as exposed if they were released after daily total dissolved gas levels reached 120% at the Warrendale site and unexposed otherwise.

Survival of the exposed and unexposed groups was measured (1) between the release site and the Astoria subarray (lower river, denoted S_R), and (2) between the Astoria subarray and Willapa Bay subarray (plume region, denoted S_P; Figure 2.2). Survival in each segment for exposed and unexposed IR and T fish, and a single detection parameter for each subarray, was estimated using the Cormack-Jolly-Seber (CJS) live-recapture modeling framework, implemented with the RMark package in R (Lebreton et al. 1992, White & Burnham 1999, R Development Core Team 2011, Laake 2012). Profile-likelihood confidence intervals (95%) for the survival estimates were also calculated with the RMark package. We used the median ĉ method, implemented in the program MARK, to evaluate the model for overdispersion, a condition where the sampling variance exceeds the expected theoretical variance due to violations of CJS assumptions, and adjusted the parameter variances to avoid overestimating the precision of the model parameters (White & Burnham 1999, Burnham & Anderson 2002). We used data from an ancillary tag life study in 2011 and program ATLAS methods[3] to correct survival estimates for possible tag failure during migration to Lippy Point (Lady et al. 2012).

In 2011, as a refinement to a long-term survival study that began in 2006, a subarray was placed at Sand Island, seaward and adjacent to the Astoria subarray. Because the median difference in detection times between the two

[3] See Appendix A for details

subarrays for those smolts detected on both arrays was only 2.8 hours (SE = 0.25), detections at Sand Island were combined with the Astoria subarray detections in the analyses reported here (Figure 2.2).

Calculating daily survival rates (henceforth, survival rates) in the lower river (S_{DR}) and plume (S_{DP}) required the group travel times in the lower river (T_R) and plume (T_P). We define T_R as the median of individual lower river travel times, in days, which were calculated by subtracting the release date from the time of entry into the plume, where entry time is taken as the final detection time of an individual at Astoria or Sand Island. T_P is the median of individual plume travel times, which were calculated by subtracting the time of plume entry from the time of plume departure (the final detection of an individual at Willapa Bay). We scaled the survival estimates (S_R and S_P) and their 95% confidence intervals by travel time (T_R and T_P) to obtain the river and plume survival rates, S_{DR} and S_{DP}:

$$S_{DR} = S_R^{\frac{1}{T_R}}$$

$$S_{DP} = S_P^{\frac{1}{T_P}}$$

Standard errors for survival rates were calculated using the Delta method

(Dorfman 1938). The effect size of exposure to high TDG levels (TDG ≥ 120%) on survival and survival rates in each segment was calculated by subtracting survival or the survival rate of the unexposed group from the exposed group. Thus, a negative effect size indicated reduced survival in the exposed group relative to the unexposed group.

In estimating survival, we made the standard CJS assumptions that (1) every tagged individual has equal probability of survival and detection following release, (2) sampling periods are instantaneous, (3) emigration is permanent, and (4) that tags are not lost. We also assumed that (a) similar proportions of the groups departing the Columbia River swam north (Miller et al. 1983) and (b) the cross-shelf extent of the subarrays at Willapa Bay and Lippy Point were sufficient to bound the early marine migratory path (Bi et al. 2007, Trudel et al. 2009, Peterson et al. 2010; see also Rechisky et al. 2012, Brosnan et al. 2014).

Total dissolved gas levels.

Hourly total dissolved gas levels are recorded by automated water quality monitoring stations at (1) Cascade Island, located immediately below Bonneville dam, (2) Warrendale, OR, located 9 km downstream of the dam, and (3) Camas/Washougal, located 40 km downstream (Tanner et al. 2011; Figure 2.2). Hourly TDG and Bonneville Dam spill data are provided courtesy of the U.S. Geological Survey (USGS 2013), and quality-assurance measures for these data

are described in Tanner et al. (2011).

High discharge through the Bonneville Dam spillway destroyed the Cascade Island monitoring site on May 18th, 2011, just prior to the release of 280 acoustic tagged fish at the Bonneville Dam smolt monitoring facility (Tanner et al. 2011; Table 2.1). In lieu of field observations, we obtained estimated hourly TDG at Cascade Island from SYSTDG, a sophisticated model used by the U.S. Army Corp of Engineers to predict TDG levels and support spill management decisions in the Columbia River basin (Schneider & Hamilton 1999, L. Hamilton, U.S. Army Corp of Engineers, personal communication, 2013).

Oregon and Washington law dictate different methods for calculating daily total dissolved gas and we calculated daily TDG using both methods. Using the Oregon methodology, we averaged the twelve highest hourly values per calendar day from April 1st though June 15th, 2011 (OSA 2003). Using the Washington methodology, we averaged the 12 highest consecutive readings in each calendar day over the same period (OCR 2003). The two methods produce nearly identical results; henceforth, reference to daily TDG in this article refers to daily TDG calculated using the Oregon method. The Oregon and Washington TDG limits do not apply when the flow exceeds the 10 year, 7 day average flood flow, the '7Q10' criterion (OSA 2003, OCR 2003). Dates when the 7Q10 criterion was exceeded in 2011 were retrieved from the U.S. Army Corp of Engineers' 2011

Dissolved Gas and Water Temperature Report (USACOE 2011).

Results

Median ĉ of the survival model was 1.17 (SE = 0.09). This is weak evidence for overdispersion and indicates limited violations of our assumptions and good structural fit of the model (Burnham & Anderson 2002). Tag-life adjusted survival, travel times, survival rates, and effect sizes on lower river and plume survival and survival rates are shown in Table 2.2 (lower river) and Table 2.3 (plume). Detection probabilities on each array, survival estimates, and tag-life adjusted survival estimates are in Table 2.4. We considered effect sizes to be significant if the 95% confidence intervals did not include zero (Figure 2.3). Survival to Lippy Point, provided for completeness in Table 2.4, are minimum estimates obtained by setting the detection probability at Lippy Point at 1. Fixing this parameter had no appreciable effect on the remaining parameters and does not affect our results and conclusions.

Table 2.2. Lower river survival (S_R), daily survival (S_{DR}), travel time (T_R; days), and effect sizes (ES_R, ES_{DR}).

Group	S_R (SE)	ES_R (SE)	T_R	S_{DR} (SE)	ES_{DR} (SE)
In-river, exposed	0.82(.04)	-0.02(.06)	2.7d	0.93(.02)	-0.06(.02)
In-river, unexposed	0.84(.04)		15.4d	0.99(0.0)	
Transport, exposed	0.88(.05)	0.08(.07)	3.3d	0.96(.02)	0.01(.02)
Transport, unexposed	0.80(.05)		4.6d	0.95(.01)	

Table 2.3. Plume survival (S_P), daily survival (S_{DP}), travel times (T_P; days), and effect sizes (ES_P, ES_{DP}).

Group	S_P (SE)	ES_P (SE)	T_P	S_{DP} (SE)	ES_{DP} (SE)
In-river, exposed	0.28(.05)	-0.01(.07)	4.2d	0.74(.03)	-0.15(.03)
In-river, unexposed	0.29(.04)		10.3d	0.89(.01)	
Transport, exposed	0.19(.05)	0.11(.07)	4.0d	0.66(.05)	-0.18(.06)
Transport, unexposed	0.07(0.04)		14.9d	0.84(.03)	

Table 2.4. Segment-specific estimates of detection, survival, and survival adjusted for possible tag failures. Lippy Point data are provided for completeness. Detection probability at Lippy Point was fixed at 1, which provides a minimum estimate of coastal survival. No tags from the Transport, Unexposed group were detected at Lippy Pt.

Segment	Detection probability (SE)	Group	Survival	Adjusted survival (SE)
Lower River (to Astoria)	0.96 (.02)	In-river, Exposed	0.80 (.03)	0.82 (.04)
		In-river, Unexposed	0.82 (.03)	0.84 (.04)
		Transport, Exposed	0.86 (.04)	0.88 (.05)
		Transport, Unexposed	0.78 (.05)	0.80 (.05)
Plume (to Willapa Bay)	0.71 (0.08)	In-river, Exposed	0.28 (.05)	0.28 (.05)
		In-river, Unexposed	0.29 (.04)	0.29 (.04)
		Transport, Exposed	0.19 (.05)	0.19 (.05)
		Transport, Unexposed	0.07 (.04)	0.07 (.04)
Coastal Ocean (to Lippy Pt.)	1.0	In-river, Exposed	0.14 (.05)	0.16 (.04)
		In-river, Unexposed	0.28 (.06)	0.29 (.06)
		Transport, Exposed	0.12 (.09)	0.12 (.09)
		Transport, Unexposed	0.00 (.00)	0.00 (.00)

Point estimates of the effect of high TDG exposure (≥120%) on lower river and plume survival were close to zero for in-river and positive for transported fish, and in all cases the confidence intervals included zero (Figure 2.3). However, the lower river and plume residence times of exposed groups were shorter than those of the unexposed groups, presumably because of the higher river flows; the exposed group of in-river migrants passed through the lower river in 2.7 days and the plume in 4.2 days, whereas the unexposed in-river groups made the same passages in 15.4 and 10.3 days, respectively. Transported fish exhibited a similar, but less extreme variation in lower river travel time: 3.3 days for the

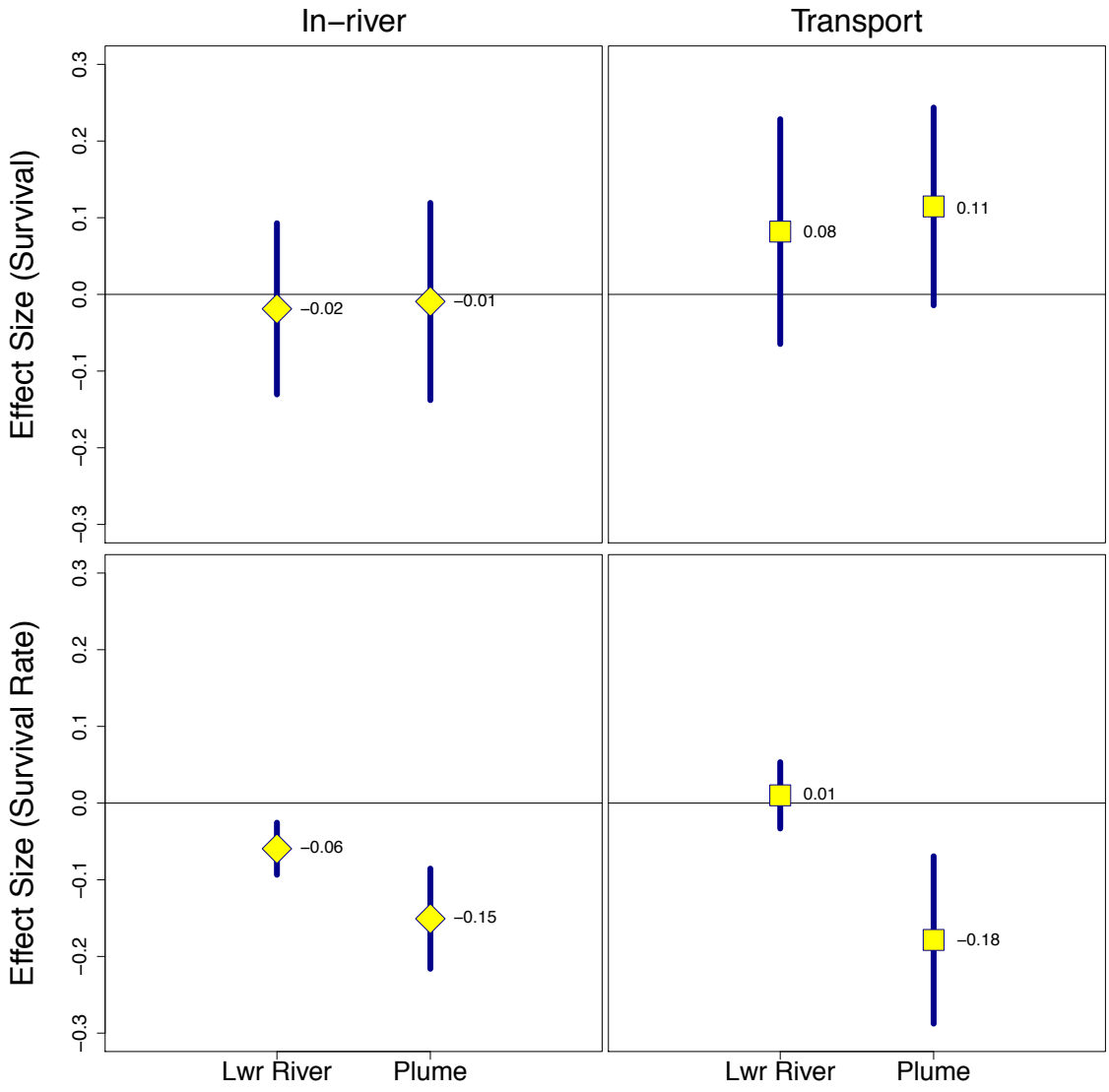

Figure 2.3. The effect size of total dissolved gas exposure on survival (top panel) of in-river (left panels) and transported (right panels) fish and the survival rate per day (bottom panels) in the lower Columbia River and plume (95% confidence intervals). A negative effect size indicates reduced survival in the exposed group relative to the unexposed group.

exposed group, and 4.6 days for the unexposed group. Differences in plume travel times were greater: 4.0 days for the exposed transported group and 14.9 days for the unexposed transported group.

Seventy-two IR fish assigned to the unexposed group and detected at the river mouth remained somewhere upriver of the Astoria and Sand Island subarrays after May 14th, when TDG reached 120% in the Bonneville Dam tailrace. Sixty-eight of these 72 subsequently crossed the river mouth by May 23rd, three crossed by May 28th, and the single remaining fish crossed on June 13th. The final two unexposed Transport fish to be detected at the river mouth crossed on May 15th. Based on back-calculation of their individual average travel speeds and the rate of decline in TDG from Bonneville Dam to the Camas/Washougal TDG monitoring station (Figure 2.1), we estimate that only the single in-river fish that crossed on June 13th was potentially exposed to TDG above 120% and we made no adjustments to the group assignments.

After scaling survival by travel time to account for the different observation intervals, the lower river survival rate was reduced by -0.06 d^{-1} (SE = 0.02) for the gas-exposed IR group relative to the unexposed group. A substantially larger reduction in survival rate of the gas-exposed IR fish was subsequently found in the plume environment, -0.15 d^{-1} (SE = 0.03), and also for the T group, -0.18 d^{-1} (SE = 0.06; Figure 2.3). The survival rate of exposed T smolts was not

significantly different from the unexposed group in the lower river.

Discussion

There is substantial prior evidence that exposure to elevated TDG levels can be harmful to aquatic organisms. They may experience gas bubble trauma (also referred to as gas bubble disease), which can produce blockages of the vascular system (emboli) and internal and external soft tissue damage, similar to 'the bends' experienced by mammalian divers, leading to direct mortality or reduced fitness (Bouck et al. 1976, Bouck 1980, Mesa & Warren 1997, Mesa et al. 2000). Gas bubble trauma induced in smolts by hydropower operations has been a recurring concern in the Columbia River basin, first in the 1960's, then in the late-1990's as spill was increasingly viewed as a means to mitigate the deleterious effects of turbine passage, and now as a large-scale operational test of the effect of FCRPS dam spill on smolt-to-adult returns has been proposed (Weitkamp & Katz 1980, Mesa et al. 2000, NMFS 2013).

Unfortunately, results from laboratory experiments are not easily translated to acute and chronic fitness effects of TDG exposure in the wild, and field surveys of GBT symptoms do not directly capture such effects (although acoustic telemetry may be able to bridge these gaps). In laboratory settings, TDG exposure can be controlled, but in natural settings, smolts may experience

multiple exposures and exposure levels that decline with depth and distance from the source and are difficult to characterize and replicate. The solubility of gas in a solution increases with pressure (Henry's Law) and for each meter increase in water depth, hydrostatic pressure compensates for approximately 10% of TDG (Colt 2012). Beeman & Maule (2006) reported that the depths of outmigrating yearling Chinook in the Snake River (below Ice Harbor Dam) and Columbia River (above McNary Dam) could provide potential hydrostatic compensation as high as 24.4% (similar studies of migration depth have not been reported for the river below Bonneville Dam). Field surveys of GBT symptoms are useful in determining their prevalence, but have limited capacity for evaluating fitness effects (Mesa et al. 2000). Such surveys are conditional on smolts surviving exposure to be sampled, and then exhibiting detectable symptoms when assayed. These challenges make it important to directly measure how much survival may be reduced in the wild following exposure to supersaturated water.

The differences in lower river survival rates reported here are consistent with previous research into the effects of TDG exposure. Mesa et al. (2000) reported an LT_{20} (time to 20% mortality) of 3-6 hours for fish held at 130% TDG for up to 11 hours, an LT_{20} of 40-120 hours among fish held at 120% TDG for up to 140 hours, and no mortalities in fish held at 110% TDG for 22 days. In a laboratory study, Mesa & Warren (1997) showed that in trials lasting up to three hours, juvenile yearling Chinook previously exposed to 130% TDG for 3.5 hours were significantly more vulnerable to predation by Northern pikeminnow (*Ptychocheilus*

oregonensis) than unexposed controls. This indirect effect may result from a reduced ability to detect and/or avoid predators due to impaired lateral line function and swimming ability (Schiewe 1974, Schiewe & Weber 1976). However, the effect was not apparent at lower levels of exposure (Mesa & Warren 1997).

In our study, only exposed IR fish that were released when TDG levels were very high at Cascade Island (>130%) exhibited a reduction in lower river survival rate relative to their unexposed counterparts. If TDG exposure was the cause, it is impossible to distinguish between rapid direct mortality (e.g., Bouck et al. 1976, Mesa et al. 2000) and reduced fitness leading to a lower survival rate (e.g., Mesa & Warren 1997). However, if the survival rate of the unexposed IR fish approximates the true survival rate for both exposed and unexposed fish, then approximately 15% of the exposed fish need to have succumbed shortly after release to realize the observed 80% lower river survival.[4] This compares reasonably well with an LT_{20} (time to 20% mortality) of 3-6 hours for fish held at 130% TDG (Mesa et al. 2000).

Lower initial exposure levels and decline in TDG with distance from the dam may explain the insignificant difference in lower river survival rates between the transported groups. Transported smolts were released approximately ten

[4] The full calculation is contained in Appendix A.

kilometers downstream of the in-river smolts, placing them closer to water with lower levels of gas saturation, and potentially providing some reduction in GBT symptoms and relief from direct mortality (Weitkamp & Katz 1980, Hans et al. 1999). Even at the maximum estimated exposure level of the transported smolts, 126% TDG, the time to mortality would be extended relative to exposures above 130% (Bouck et al. 1976, Mesa et al. 2000).

Long-term, chronic effects on smolt fitness following TDG exposure have not been well studied at the spatial and temporal scales represented in this analysis. Similar to divers suffering decompression sickness, smolt mortality following TDG exposure may occur in both an acute phase[5] where mortality is directly caused by embolism or emphysema blocking blood flow to critical organs, and a chronic phase where mortality may indirectly result from predators targeting smolts with reduced fitness, e.g. impaired motor skills or brain function, or reduced disease resistance. In the plume, survival rates of exposed transport and in-river fish were reduced relative to the unexposed groups (Figure 2.3). This suggests that chronic effects of GBT, which are difficult to quantify in laboratory settings, may persist into the plume and have important effects on survival.

If there was a long-term chronic effect due to elevated TDG exposure, it probably

[5] Acute and chronic effects on survival should not be confused with chronic (110% TDG) and acute (≥120% TDG) exposures, as defined by Mesa et al. (2000).

did not result from the additional stress of acclimating to saltwater. Nebeker (1979) reported that juvenile Chinook salmon transferred to saltwater and observed for ten days after exposure to supersaturated freshwater at 108, 110, 113, 115, and 117% TDG for 21 days recovered quickly and experienced no further mortalities, although the sample size was small (n = 2 to 10). Exposed fish may remain physiologically compromised and experience reduced survival in natural settings, despite the absence of external symptoms and declines in mortality in laboratory settings. Nebeker et al.'s (1979) protocol would not detect predation on unfit but alive smolts.

Holding fish for tagging in tanks containing flow-through river water had the advantage of exposing fish to the same water quality conditions as their untagged counterparts, including those found arriving at Bonneville Dam exhibiting symptoms of GBT (FPC 2013a), but may represent a worst-case exposure scenario. TDG levels in the Bonneville Dam forebay reached 122% during the tagging period and exposure to forebay-sourced water in the tanks resulted in symptoms of gas bubble trauma in 17 IR fish that were found dead on May 28th and examined by the Lower Columbia River Fish Health Center (CBR 2013). This was the only large mortality event and does not appear to have affected transported fish held at Lower Granite Dam, where TDG levels in the forebay peaked at 107% and there were no reported incidences of gas bubble trauma in arriving fish (CBR 2013, FPC 2013a; the barges used for transporting smolts from Lower Granite Dam for release below Bonneville operate gas-

stripping equipment to prevent GBT during transit).

It is challenging to distinguish among the environmental factors that may affect smolt survival in the Columbia River and plume due to simultaneous variation among many variables and the difficulty of conducting controlled experiments in nature (but see Rechisky 2012, 2013, 2014, where such experiments were conducted). Total dissolved gas levels co-vary with other factors thought to potentially affect smolt survival, such as temperature, turbidity, disease, and emigration timing. However, our observations are consistent with what is known about the effects of TDG exposure and it is a parsimonious explanation for reduced survival rates. In contrast, water temperature, measured at the Warrendale monitoring station (Figure 2.2), was between 8° and 13° C when IR and T smolts were released, well below lethal levels (22°-25° C) and levels affecting growth and mortality in juvenile Chinook (ca. 15° C; Richter & Kolmes 2005). Turbidity measured at Bonneville Dam increased between releases of unexposed and exposed groups, which would generally be expected to improve, not reduce, smolt survival (Gregory & Levings 1998, CBR 2013). Additionally, there were no clear differences in disease prevalence on dates when exposed and unexposed IR smolts were collected for tagging, and prevalence may have declined between collections of unexposed and exposed T smolts (FPC 2013b). The mean percentage of disease recorded at Bonneville Dam when unexposed IR smolts were collected was 1.25% (SE = 0.95; n = 4 days) and 1.00% (SE = 0.58; n = 3 days) when exposed smolts were collected (no data was recorded on

the fourth collection day). The mean percentage of disease recorded at Lower Granite Dam when unexposed T smolts were collected was 3.33% (SE = 1.17; n = 2 days) and 0.00% (n = 2 days) when exposed T smolts were collected.

There do not appear to be any published studies of the effect of emigration timing on smolt survival in the lower Columbia River. Scheuerell et al. (2009) examined the effect of emigration timing on smolt-to-adult returns and concluded that there were higher returns among smolts migrating in early- to mid-May relative to mid-June, although there was significant interannual variability. In the years of their study, 1998-2003, it appears that smolts released on the same late-April/early-May dates as in our study could have had lower, similar, or improved returns over those released in mid- to late-May. The applicability of Scheuerell et al's (2009) results to lower river survival, as opposed to adult returns measured several years after ocean entry, is unknown.

Our results suggest that TDG levels resulting from spill at Bonneville Dam do not affect lower river survival except during periods of very high spill. Such spill levels are probably unavoidable during periods when high flow exceeds powerhouse capacity, and this is reflected in the exception to the state TDG limits that came into effect on May 21st, 2011, when the 10 year, 7 day average flood flow was exceeded (USACOE 2011, OCR 2003, OSA 2003). Furthermore, the exposed IR fish that had a lower daily survival rate in the river were held in tanks containing

flow-through water and had reduced opportunity for depth compensation. Thus, while the effect on the lower river survival rate under these relatively extreme conditions was measurable (-0.06 d^{-1} (SE = 0.02)), it may also represent only a worst-case exposure scenario.

The reductions in plume survival rates among exposed IR and T groups are notably larger than in the lower river, 0.15 d^{-1} (SE = 0.03) and 0.18 d^{-1} (SE = 0.06) respectively, and may have more important ecological and management implications. There has been little work on chronic effects of TDG exposure on smolt survival beyond monitoring the progression of visible symptoms and mortality after return to saturated water in laboratory settings; this is likely due to the cost and technical difficulty of conducting such field experiments. However, the chronic (sublethal) effects of emboli and tissue damage (e.g., pain, neurological deficit) resulting from decompression sickness are well documented in human divers, and it is plausible that similarly reduced fitness could result in indirect mortality among fish in natural settings.

Importantly, it is only when travel time is taken into account that any exposure effect becomes apparent. There were no evident differences in overall survival between geographically fixed receiver arrays for exposed and unexposed fish in the lower river or plume. This highlights the importance of considering the period of observation in such studies.

In summary, we measured reduced survival rates in the lower Columbia River and plume among groups of acoustically tagged fish released when total dissolved gas levels were at levels known to be harmful. It appears that at high levels of initial TDG exposure (>130%), an initial acute mortality phase is followed by a chronic mortality phase, which is expressed at least as far as the Willapa Bay subarray that was reached some 7 days post-release. At lower levels of initial exposure, acute mortality appears limited, consistent with previous research, but a chronic mortality phase may exist. Because our analysis is based on observational data relating exposure levels to subsequent survival rates in the wild, our results are potentially confounded by other unidentified differences that co-vary with the differing release times of exposed and unexposed groups. A formal experiment using simultaneous releases of smolts exposed to different levels of TDG along with control groups of unexposed smolts could easily be performed using the same techniques described here and in Rechisky et al. (2012, 2013) to objectively clarify how survival rates in the lower reaches of the Columbia River and the coastal ocean are affected by TDG exposure.

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CHAPTER 3

AN INDIVIDUAL-BASED MODEL EVALUATION OF POSSIBLE MIGRATION STRATEGIES FOR YEARLING CHINOOK SALMON IN THE COLUMBIA RIVER PLUME

Abstract

An individual-based model (IBM) was constructed to evaluate two strategies that juvenile yearling Chinoook salmon (smolts) are hypothesized to use while migrating north through the Columbia River plume: maximize growth, or minimize plume occupancy time (and thus exposure to high predation pressure in the plume) through selective use of local currents. Maximizing growth better replicated migratory patterns observed in acoustic telemetry studies. Selective use of currents did little to reduce travel time to an array of acoustic receivers north of the river mouth, suggesting that there may be little selective pressure for this strategy. Approximately 18% of model smolts were advected off the continental shelf and did not cross the receiver array north of the river mouth. Yearling Chinook smolts are believed to be restricted to the shelf, but surface trawls and acoustic receivers do not extend offshore to validate or reject this model prediction. If real, temporarily trading improved feeding opportunities for reduced exposure to the predation pressures near the river mouth may affect survival. Future modeling efforts should incorporate predator and prey data in

habitat selection decisions evaluated over a time horizon extending through the marine critical period to the start of winter.

Introduction

The Columbia River plume is a dynamic coastal feature that juvenile yearling Chinook salmon (*Oncorhynchus tshawytscha*), henceforth termed 'smolts,' must navigate during the earliest stage of their marine migration. Previously, the plume was hypothesized to be a refuge from predators and a rich feeding ground (Casillas 1999), but more recent research suggests that the plume is predator rich and that survival is low in the plume relative to adjacent estuarine and ocean habitat (Collis et al. 2002, Anderson et al. 2004, Lyons et al. 2005, Emmett et al. 2006, Porter et al. 2012). Due to the perceived importance of the early marine period, there has been a persistent interest in the interaction between the Columbia River plume environment and juvenile salmon migration and survival, particularly as to how migration and survival may be affected by river dynamics (Jay et al. 2009, Burla et al. 2010a, Miller et al. 2013).

Determining the effects of changing plume conditions requires some understanding of the elements of the plume environment that smolts use during this phase of their migration. We can envision two strategies that smolts may adopt. The first is to select habitat that maximizes growth. This strategy would be expected to reduce availability to size-selective predators while contributing to the growth necessary for them to survive their first winter at sea. This strategy is consistent with the critical size, critical period hypothesis which posits that the adult return rate of salmon is influenced first by predation-driven mortality at

ocean entry, then by starvation-driven mortality during the following winter that results from a failure to build minimum energy reserves (Beamish & Mahnken 2001).

A second plausible strategy is to selectively use local coastal flow to minimize head current while migrating north. This would speed northward passage, reducing the period of exposure to predation in the plume region. Brosnan et al. (2014) demonstrated that survival of groups of yearling Chinook released to migrate through the plume is negatively related to their travel time, so this strategy could offer fitness benefits. This behaviour has also been observed in the field; stereovideographic studies in tributaries of the Fraser River reveal that adult sockeye salmon (*Oncorhynchus nerka*) migrating upriver selectively travel in lower current (Standen et al. 2004), and may exploit counterflowing eddies (Hinch & Rand 2000). Juvenile salmon are believed to similarly exploit turbulent flow during their downstream migration (Coutant & Whitney 2000, Tiffan et al. 2009).

Although it is technically feasible to directly observe the fine-scale movements of juvenile salmon in coastal marine waters, it is cost-prohibitive. Instead, I used an individual-based model (IBM) to evaluate which strategy produces results consistent with observed migration patterns. The model was implemented in NetLogo, a sophisticated and popular Java-based software for individual-based

modeling (Wilenski 1999) and draws on simulation output (salinity, temperature, and current) from the Virtual Columbia River model developed by the Center for Coastal Margin Observation and Prediction. The IBM doesn't test the effects of different strategies on plume survival, but rather which, if any, of the plausible strategies reproduces migratory patterns observed in acoustic telemetry studies of juvenile yearling Chinook.

Materials and Methods

The model draws on detections of acoustic tagged juvenile yearling Chinook (*Oncorhynchus tshawytscha*) and oceanographic simulations from the 2009 spring outmigration. This dataset was chosen because tagged smolts were released from early-April through May, covering a wide range of spring ocean conditions.

Briefly, in 2009 VEMCO V7-2L acoustic tags were surgically implanted in 1,370 Columbia River Basin juvenile yearling Chinook. Smolts originated from the Cle Elum Supplementation and Research Facility (CSERF) and Dworshak National Fish Hatchery (DNFH). CSERF acoustic tagged smolts were released downstream at the Chandler Juvenile Monitoring Facility, and DNFH smolts were released in the vicinity of the hatchery, or barged and released below Bonneville Dam. Acoustic receivers deployed across the river at Astoria Bridge and across the continental shelf at Willapa Bay detected the passage of tagged smolts. Smolts detected on both the Astoria and Willapa Bay sub-arrays (N = 103) were

used to calculate plume residence time, and the cross-shelf distribution at Willapa Bay. Greater detail on the tagging procedures and acoustic array used to track tagged smolts can be found in Brosnan et al. (2014). A complete explication is available in Porter et al. (2010).

Individual-based model description

The model was implemented in NetLogo v.5.0.4, a Java-based software for individual-based modeling (Wilenski 1999). The model is described here using the 'Overview, Design concepts, and Details,' or ODD, protocol of Grimm et al. (2010).

1. Purpose

The purpose of the model was to compare two hypothesized habitat selection strategies used by smolts during their northward migration through the Columbia River plume: do smolts select habitat to maximize growth, or attempt to minimize head currents to more quickly escape the plume?

2. Entities, state variables, and scales

There were two entities in the model, ocean cells and model smolts. Each ocean cell had six state variables: salinity, temperature, current velocities (x- and y-),

depth, and a depth-dependent representation of feeding conditions. There were two breeds of model smolt, defined by their habitat selection rules in the ocean (Table 3.1). Each smolt, regardless of breed, had five state variables: fork-length, weight, optimal swimming speed, heading, and a binary variable indicating whether the smolt was in estuarine or ocean waters.

Table 3.1. Model smolt breeds.

Estuarine Navigation → ***Ocean Navigation*** ↓	*Negative Rheotaxis*
Maximize growth	MaxGnr
Minimize head currents	MinCnr

Simulations ran for 70 days in 1-hour steps (1,680 model steps). The model world origin was in the top-left grid cell, at position 3601 255000mE, 369500mN (Oregon State Plane coordinates, North American Datum of 1927). The model world extended 100 km east of the origin and 200 km south in a grid with 0.5km x 0.5 km cells; roughly the distance that a 130 mm smolt (the smallest size tagged) would swim in one hour at 1 body length per second. This area encompasses the lower Columbia River estuary and plume region.

3. Process overview and scheduling

At every step, eight smolts of each breed were introduced into the model (total N = 10,008). To permit the last smolts introduced into the model sufficient time to migrate past Willapa Bay, the introduction of model smolts ended at step 1,250.

At each step, the ocean cells updated their salinity, temperature, current velocities, and prey availability. Subsequently, each smolt calculated its weight- and temperature-dependent optimal swimming speed, evaluated whether it was in estuarine water (cell salinity < 27 PSU) or marine water (cell salinity > 27 PSU) and moved accordingly (see 7. Submodels for a description of movement rules). Once all smolts executed their move, the model stepped forward (Figure 3.1).

4. Design Concepts

Pearcy (1992) is widely credited with the hypothesis that the year class strength of returning salmon is established during the early marine life history, including the period of plume residency. Yearling Chinook departing the Columbia River must travel through the river plume, the dynamics of which are affected by hydropower-regulated river discharge and wind-driven currents (Burla et al. 2010b). Survival in this region is presumably affected by the migratory strategy adopted by smolts, and insight into the manner that individual smolts interact with the plume environment while migrating, revealed by patterns in their distribution

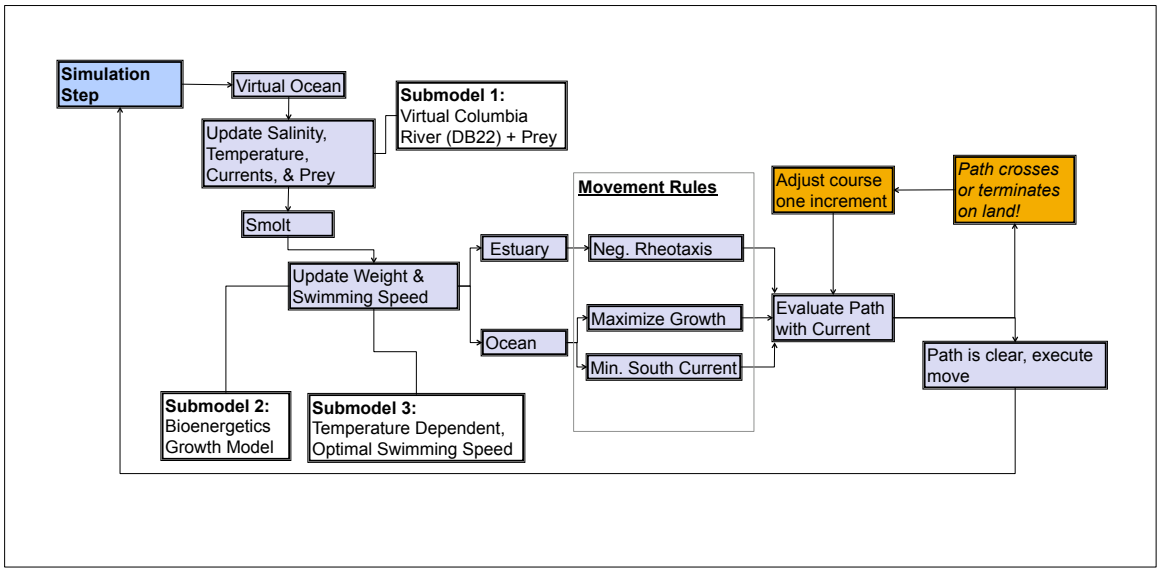

Figure 3.1. Process overview diagram. The origin is at the top left blue box entitled ‘Simulation Step.’ Purple boxes delineate the process, orange boxes delineate the algorithm for ensuring smolts do not cross or move to land, and white boxes indicate sub-model routines.

across an acoustic array, could be used to evaluate the impact of changing oceanographic and river conditions.

Model smolts adapt to changes in themselves and their environment by selecting a weight and temperature-dependent optimal swimming speed and orienting towards habitat consistent with their breed objectives; maximize growth, or minimize head current during their directed northward migration. Implementing these behaviors requires a number of assumptions.

(1) In the model estuary and into the plume, smolts employ negative rheotaxis. Upregulation of thyroxine in response to changing light conditions stimulates negative rheotaxis, leading smolts to travel downstream (Cooke et al. 2011); this behaviour is assumed to persist to the ocean. (2) Smolts are also assumed to have a compass sense and (3) are able to detect gradients in temperature, salinity, current, and prey availability. The specific mechanisms by which smolts sense these variables are not modeled, but field and laboratory observations indicate that smolts can sense gradients in the orientation and intensity of magnetic fields (Putnam et al. 2014), flow (Standen et al. 2004, Kemp & Williams 2008), temperature (Hinke et al. 2005), and salinity (Healey 1980). Their presence in trawls is also positively correlated with chlorophyll concentration and plankton abundance (Bi et al. 2007, Bi et al. 2011, Yu et al. 2012). (4) Smolts are also assumed to begin a directed northward migration shortly after reaching the

ocean, an assumption that is strongly supported by decades of U.S. and Canadian coastal trawl surveys (Miller et al. 1983, Fisher & Pearcy 1995, Trudel et al. 2009). (5) To allow the model to be collapsed into 2 spatial dimensions, vertical migrations are assumed not to significantly affect horizontal progress.

A representation of declining prey availability with distance from shore was drawn from Peterson et al.'s (2010) description of three cross-shelf zones. In the model, prey is represented to the model fish through the proportion of maximum consumption (bioenergetics parameter 'p_C_{max}'; Brodeur et al. 1992), values of which are drawn from one of three beta distributions representing inshore waters (depth ≤ 50 m, mean 'p_C_{max}' = 0.8), mid-shelf waters (50 m < depth ≤ 150 m, mean 'p_C_{max}' = 0.6) and outer shelf/open water (depth > 150 m, mean 'p_C_{max}' = 0.02). Although the assignment of 'p_C_{max}' is consistent with the biomass estimates in Peterson et al. (2010) and assumptions about the volume of water searched by a transiting salmonid (Mazur & Beauchamp 2003), they are a characterization, rather than a replication, of actual feeding conditions.

Stochasticity in the model appears in the assignment of a fork length to each model smolt, 'p_C_{max}' values assigned to the cells, and the direction of heading change used to iteratively search for a clear swimming path. Each behavior was simulated in a separate model run with a starting seed of 0 to ensure reproducibility. NetLogo does not have the capacity to draw from a beta

distribution to assign a value for 'p_C_{max}' to each cell. Instead, 1000 values for each zone were drawn in R after setting a common seed, 0. These values were written into the NetLogo model and assigned randomly to grid cells in each zone at every step.

At each step, the model observed and recorded each smolt's unique identification number, breed, size, weight, local flow variables, heading, optimal swimming speed, and model coordinates. Detection simulations and all post-run analyses were conducted in R (R Core Development Team 2011).

5. Initialization

The model initialized on April 16th, 2009 with flow environment variables, depth, and the simplified representation of the prey field. Smolts were initialized each step in the north and south channel of the Columbia River at Astoria Bridge. Smolt fork length was assigned by drawing randomly from fork lengths of tagged smolts detected at Astoria and Willapa Bay in 2009. The fork length (FL) at tagging was adjusted for growth between release and detection at Astoria by

$$FL = FL_{tag} + 1.05 * T_{riv}$$

where FL_{tag} is the measured fork length of the tagged smolt at the time of tagging, T_{riv} is the tagged smolts travel time from release to plume entry, and 1.05 (mm d^{-1}) is observed daily growth rate in the Columbia River (Fisher & Pearcy 1995).

6. Input Data

The flow environment data for each ocean cell at each time step was imported from DB-22, a database of Virtual Columbia River (VCR) model simulations. The VCR was built by the Center for Coastal Margin Observation and Prediction (CMOP) using SELFE, an open-source, community-supported code designed for the effective simulation of 3D baroclinic circulation in the Columbia River estuary and plume that uses semi-implicit finite-element/volume Eulerian-Lagrangian algorithms to solve the Navier-Stokes equations on unstructured triangular grids (Zhang & Baptista 2008). DB-22 contains flow data at 90-second intervals from the surface to the seafloor.

To reduce computational demands, flow data at 4 m, 8 m, and 12 m for each cell in the model were extracted from DB-22 in fifteen-minute intervals and then averaged and reformatted in R to create single hourly values readable by NetLogo. The choice of depth intervals is based on Emmett et al.'s (2004) finding that smolts in the plume region are found in the upper 12 m of the water column.

7. Submodels

Submodel 1: Length-weight regression

Length-weight conversions were made using the regression model:

$$W = e^{-14.075} * FL^{3.514}$$

Where W is weight (g) and FL is fork length (mm), and -14.075 and 3.514 are fitted parameters with SE = 0.128 ($t = -110.4$, $p << 0.01$) and SE = .025 ($t = 142.7$, $p << 0.01$), respectively. This is an empirical model fitted to Columbia River basin hatchery-origin yearling Chinook smolt length-weight data collected by NOAA researchers trawling at three transects in the Columbia River plume region (Columbia River, Grays Harbor, and Willapa Bay) in May and June 2008-2011 (C Morgan, NOAA, personal communication, 2013). The model was fitted to the data using the nonlinear least squares function provided in the R *stats* package (R Development Core Team 2011).

Submodel 2: Optimal Swimming Speed

Optimal swimming speed was calculated using the formula described in Stewart

(1983) and parameterized in Stewart and Ibarra (1991):

$$U_{opt} = ACT * \left(W^{0.13}\right) * e^{0.0405*T}$$

Where T is temperature and a state variable of the cell and W, weight, is a smolt state variable. ACT is a parameter from the bioenergetics submodel described below.

Submodel 3: Bioenergetics

Growth-seeking smolts evaluate potential habitat using a bioenergetics model that draws on each cells temperature and available proportion of maximum consumption to estimate growth. The bioenergetics submodel uses the 'Wisconsin model' bioenergetics equation sets (Hanson et al. 1997; Table 3.2) for consumption (eqn. 3), respiration (eqn. 1), egestion and excretion (eqn. 2). The equations are parameterized with values from the literature on Pacific salmon bioenergetics (Table 3.3). Prey energy density, Q_f, is a single global parameter. A complete description of the bioenergetics submodel and results from a Latin Hypercube sensitivity analysis and model validation exercise are described in Appendix B.

Table 3.2. Bioenergetics equations (Hanson et al. 1997).

Consumption	$C = C_{max} * p\_C_{max} * f(T)$ $C_{max} = CA * W^{CB}$ $f(T) = K_A * K_B$ $K_A = \frac{CK1 * L1}{1 + CK1 * (L1 - 1)}$ $L1 = e^{G1 * (T - CQ)}$ $G1 = \frac{1}{CTO - CQ} * \ln\frac{0.98 * (1 - CK1)}{CK1 * 0.02}$ $K_B = \frac{CK4 * L2}{1 + CK4 * (L2 - 1)}$ $L2 = e^{G2 * (CTL - T)}$ $G2 = \frac{1}{CTL - CTM} * \ln\frac{0.98 * (1 - CK4)}{CK4 * 0.02}$
Respiration	$R = RA * W^{RB} * f(T) * ACTIVITY$ $S = SDA * (C - F)$ $f(T) = e^{RQ * T}$ $ACTIVITY = e^{RTO * VEL}$ if $T > RTL$, $VEL = RK1 * W^{RK4}$ if $T \leq RTL$, $VEL = ACT * W^{RK4} * e^{BACT * T}$
Egestion	$F = FA * T^{FB} * e^{FG * p\_CC_{max}} * C$
Excretion	$U = UA * T^{UB} * e^{UG * p\_CC_{max}} * (C - F)$

Table 3.3. Bioenergetics sub-model parameters.

	Parameter Description	Symbol	Value	Source
Consumption	Intercept: C_{max}	CA	0.303 (g g^{-1} d^{-1})	Stewart & Ibarra 1991
	Coefficient: C_{max} *vs. weight*	CB	-0.275	Stewart & Ibarra 1991
	Proportion of C_{max}	p_C_{max}	0.6	Brodeur et al. 1992
	Temperature for K_1	CQ	5 (°C)	Stewart & Ibarra 1991
	Temperature for K_2	CTO	15 (°C)	Stewart & Ibarra 1991
	Temperature for K_3	CTM	18 (°C)	Stewart & Ibarra 1991
	Temperature for K_4	CTL	24 (°C)	Stewart & Ibarra 1991
	Proportion C_{max} at θ_1	CK1	0.36	Stewart & Ibarra 1991
	Proportion C_{max} at θ_4	CK4	0.01	Stewart & Ibarra 1991
Respiration	Intercept: *R*	RA	0.00264 (g 0_2 d^{-1})	Stewart & Ibarra 1991
	Coefficient: *R vs. weight*	RB	-0.217	Stewart & Ibarra 1991
	Coefficient: *R vs. temperature*	RQ	0.06818	Stewart & Ibarra 1991
	Coefficient: *R vs. swim speed U*	RTO	0.0234	Stewart & Ibarra 1991
	Intercept: *U*	ACT	9.7 (cm s^{-1})	Stewart & Ibarra 1991
	Coefficient: *U vs. weight*	RK4	0.13	Stewart & Ibarra 1991
	Intercept: *swim speed over cutoff temperature*	RK1	1 (cm s^{-1})	Stewart & Ibarra 1991
	Cutoff temperature for activity relationship	RTL	25 (°C)	Stewart & Ibarra 1991
	Coefficient: *U vs. temperature*	BACT	0.0405	Stewart & Ibarra 1991
	Specific dynamic action	SDA	0.172	Stewart & Ibarra 1991
Egestion	Intercept: *proportion egested vs. temperature and ration*	FA	0.212	Stewart & Ibarra 1991
	Coefficient: *temperature vs. egestion*	FB	-0.222	Stewart & Ibarra 1991
	Coefficient: *p versus egestion*	FG	0.631	Stewart & Ibarra 1991
Excretion	Intercept: *proportion excreted vs. temperature and ration*	UA	0.0314	Stewart & Ibarra 1991
	Coefficient: *temperature vs. excretion*	UB	0.58	Stewart & Ibarra 1991
	Coefficient: *p versus excretion*	UG	-0.299	Stewart & Ibarra 1991
Energy Density	Intercept: *(kJ/g) versus predator body weight (W)*	a	4.18	Trudel et al. 2005
	Coefficient: *(kJ/g) versus predator body weight (W)*	b	0.0025	Trudel et al. 2005
	Conversion *(kJ to J)*	c	1000	[*Wisconsin equations require J/g*]
	Energy density of prey	Qf	4200	Trudel et al. 2005, citing Davis et al. 1998

Submodel 4: Movement rules

In the estuary, both breeds align with the current in their cell (negative rheotaxis). The time between exposure to marine waters and transition to ocean movement rules, termed ‘switch time,’ occurred six hours after first exposure to marine waters, and model smolts reverted to negative rheotaxis if they encountered estuarine water. In marine waters, smolts set their heading towards the cell north of their position with maximum growth opportunity or minimum south current that it could reach in one hour at its optimal swimming speed. If the available cells offered negative growth, the smolt oriented toward the cell offering greatest growth regardless of direction. Smolts then moved to the terminal point of a vector that was addition of their movement vector (heading, optimal speed) and the current vector in the cell they occupied.

A simple algorithm was applied at each movement to prevent a model smolt overshooting and ‘beaching’ itself, or crossing narrow peninsulas. Each smolt’s path and final destination were verified wetted. If the destination or path included dry land, smolts first searched in 45 degree heading increments for a clear path, then reduced their swimming speed and searched again. This process iterated until a clear path was found, or the smolt would move to an adjacent cell offering greatest growth or minimum south current. The direction of the heading change was chosen randomly, but only once so that heading increments were sequential. If the smolts final position was outside the north, south, or west bounds of the

model, the smolt was considered to have permanently emigrated, otherwise it grew according to the bioenergetics submodel. In the estuary, smolts were not permitted to swim east (upriver) of the model boundary.

Submodel 5: Simulated detections

Detections of model smolts on the Willapa Bay receivers were simulated by evaluating smolt paths to determine if they overlapped any of the detection zones centered on each receiver. The estimated detection range of a Vemco V7-2L acoustic tag was 400m (D. Welch, Kintama Research Services, Ltd., personal communication, 2013). Smolt paths (Euclidean lines drawn between smolt positions at each model step) that fell within a 5 km window around the boundaries of the subarray at Willapa Bay were extracted from the model output. Each line segment in this window, bounded by the smolts start and end point at each step, was evaluated using the following formula to determine whether it intersected the 400 m diameter detection zone around each receiver:

$$C = (X_0-((X_1*t)+X_2*(t-1)))^2 + (Y_0-((Y_1*t)+Y_2*(t-1)))^2 - R^2$$

where R is the receiver detection radius, t ranges from 0 to 1, and (X_0, Y_0), (X_1, Y_1), (X_2, Y_2) are the receiver locations, line start points, and line end points, respectively. Where the range of C is less than zero, or includes zero, the line

segment intersects the circle. For each line segment that intersected a receiver's detection radius, the receiver number, smolt number, and time of detection were recorded. Model detections on receivers that were lost during the 2011 season were recorded, but removed prior to analyzing the cross-shelf distributions against observed values.

Analysis

Post-run analyses, including simulated detections, were conducted in R. The cross-array distribution of detections of live, tagged smolts and model smolts was compared using a modified Cramer von-Mises test (Syrjala 2006), where the null hypothesis is that there is no difference in the distributions. Syrjala's (2006) test was calculated using the R package *ecespa*, and summary circular statistics using *circular*. The sensitivity of the cross-shelf distribution of detections and median travel time to changes in the timing of the switch between estuarine and marine behaviour and use of a fixed or variable depth-dependent 'p_C_{max}' were evaluated by running the model with fixed and variable 'p_C_{max}' at switch times of 3, 5, 6, 7, and 9 h.

Results

Plume residence and cross-shelf distribution at Willapa

Median plume residence times of the breeds, defined here as the median time

between release and first detection on the Willapa Bay subarray, differed only by a few hours. This limited its use as a distinguishing test pattern, but it proved useful for calibrating the delay between the smolts first encounter with marine water and their switch to marine behavior. Calibration experiments indicated that a 6 h delay provided the closest match between observed plume residence times (median = 4.3 d) and modeled plume residence time of MaxGnr fish (median = 4.2 d) and MinCnr fish (median = 4.1 d) and cross-shelf distributions. Sensitivity of the plume residence times and cross-shelf distribution test to the switch time are described below. A 6 h delay was used in the models run for analysis and interpretation reported below.

At a significance level of 0.05, there was no difference in the distributions of the MaxGnr breed and live, tagged smolts (*p-value* = 0.54; Figure 3.2). There was a difference in the distributions of the MinCnr breed and live tagged smolts (*p-value* = 0.02; Figure 3.2). Visual examination of the fish tracks (Figures 3.3 & 3.4) reveals a more bifurcated pattern in the MinCnr breeds tracks; they traveled close inshore when wind-driven transport was easterly (downwelling), and offshore when westerly (upwelling). MaxGnr tracks showed a similar pattern, but their sensitivity to feeding conditions, represented by variable 'p_C_{max}' values, resulted in their being retained on the shelf, and more evenly distributed.

The detection of model smolts was sensitive to the magnitude and direction of

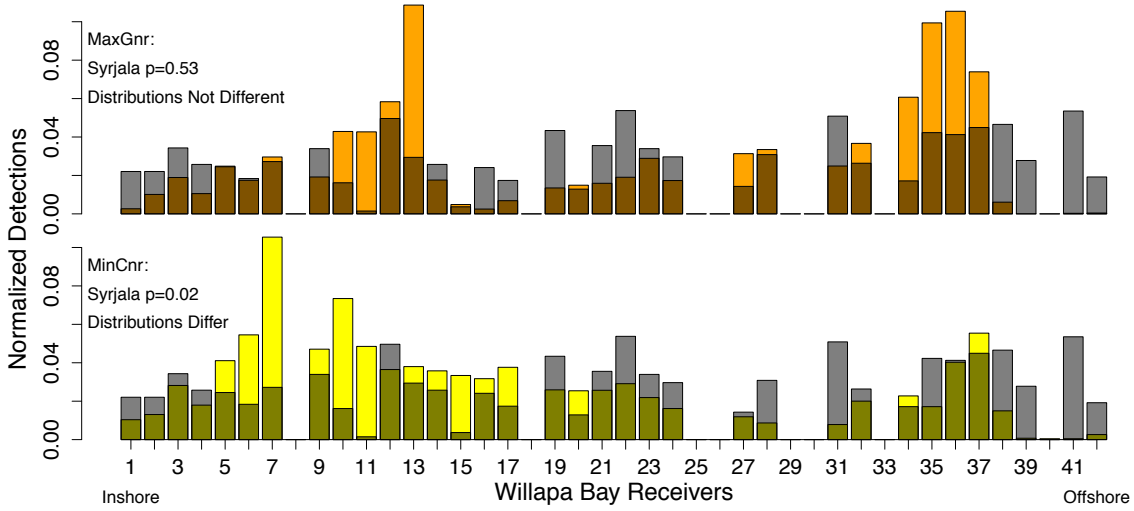

Figure 3.2. Cross-shelf distribution of detections on the Willapa Bay sub-array of receivers of MaxGnr (top panel, orange bars) and MinCnr (bottom panel, yellow bars) smolts overlaid on detections of live, tagged smolts (both panels, gray bars). Results in the top left corner of each panel are from a modified Cramer von-Mises (Syrjala 2006) test for different distributions. The MinCnr smolts appear to have a more inshore distribution across the array than observed or MaxGnr smolts, likely reflecting their use of a coast-hugging, north-flowing plume that develops with westerly winds.

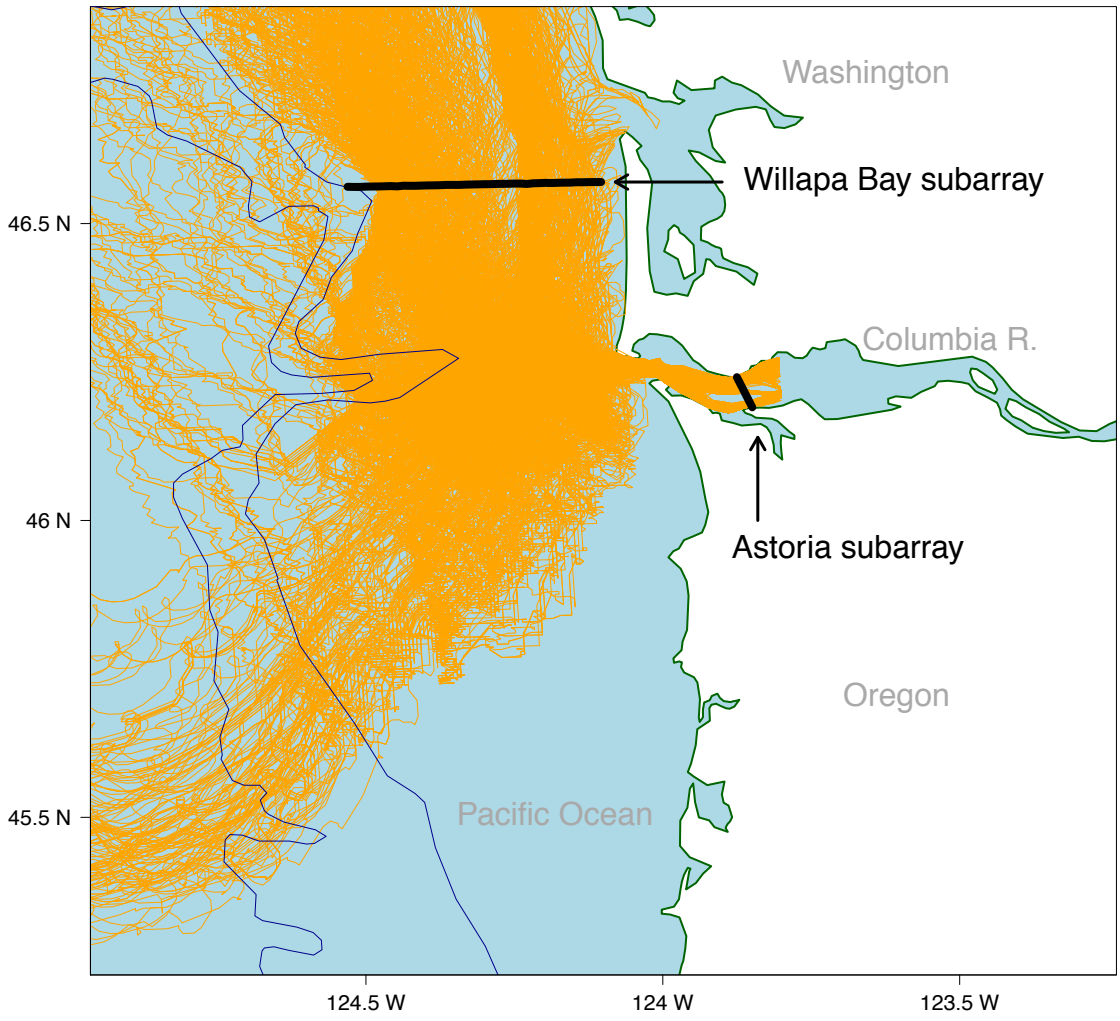

Figure 3.3. MaxGnr tracks. To reduce clutter, only the track of the first smolt released at each step is displayed. Contour lines mark the 200 m and 500 m isobaths.

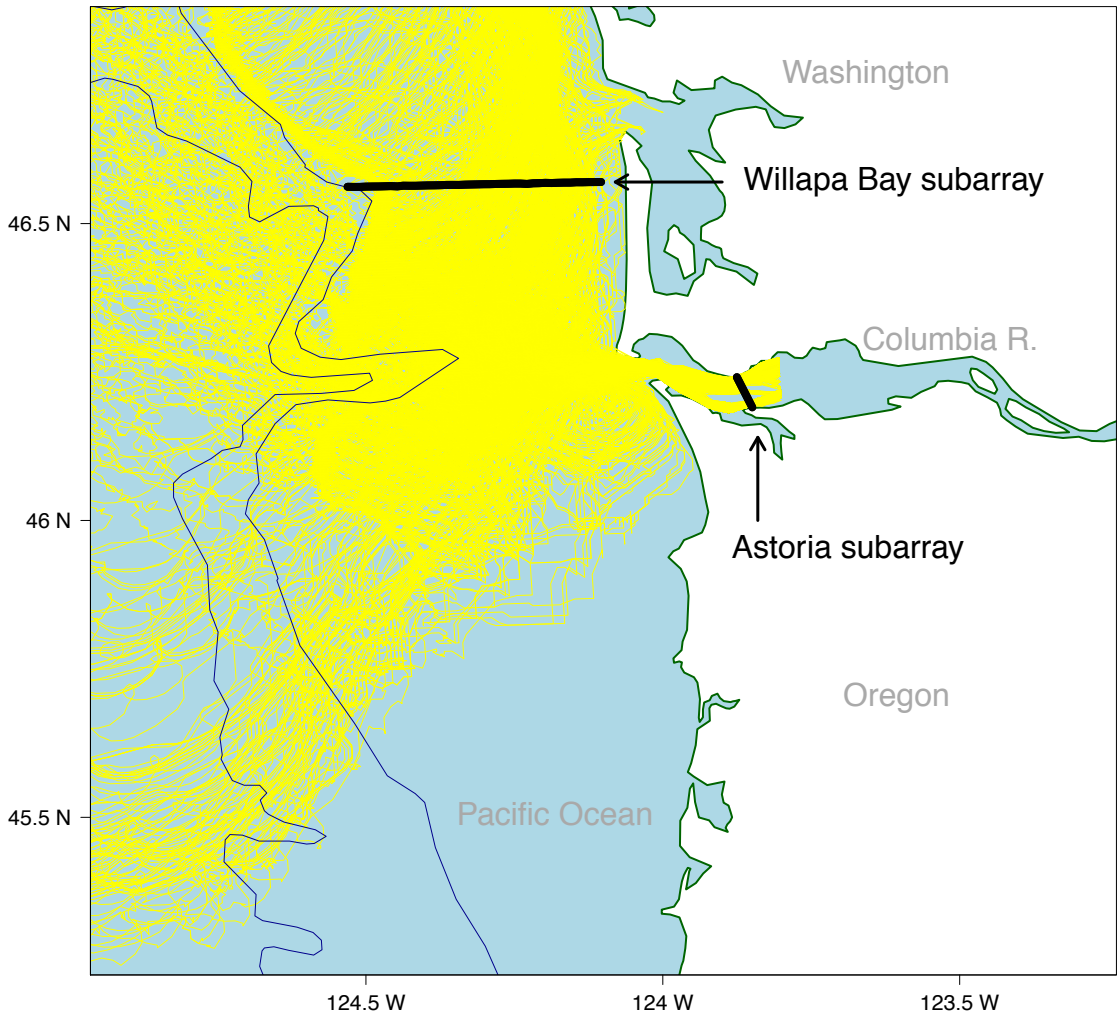

Figure 3.4. MinCnr tracks. To reduce clutter, only the track of the first smolt released at each step is displayed. Contour lines mark the 200 m and 500 m isobaths.

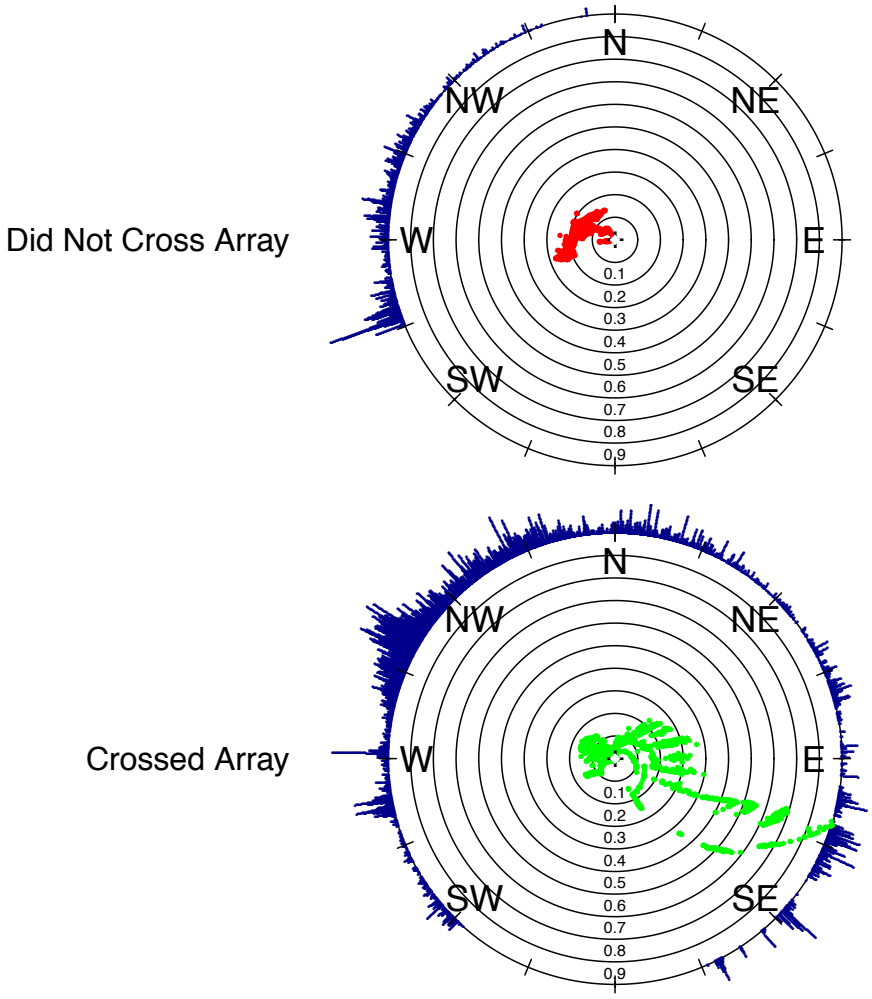

Figure 3.5. Average magnitude (represented by the distance from origin, and rescaled from 0 to 1) and direction of transport experienced by individual MaxGnr smolts that did not cross the array (top) and that crossed the array (bottom). Rescaling was performed across all smolts and results are similar for MinCnr smolts. The height of the blue bars indicates the number of smolts experiencing that average angle of transport. Smolts that did not cross the array were those experiencing stronger west to northwest transport.

wind-driven coastal transport (Figure 3.5). 8,091 (81%) of MaxGnr smolts crossed the deployed array. 1,073 smolts that crossed the array were not detected due to gaps in the array from receivers lost after deployment. 1, 917 (18%) of MaxGnr smolts did not cross the deployed array, either because they passed west of the array, or left the model before reaching the array latitude. The median of the average magnitude and direction of transport experienced by MaxGnr smolts that crossed the subarray at Willapa Bay, including those not counted as detections due to missing receivers, was 3.7 $m^3 s^{-1}$ 100 m^{-1} at 311.4 degrees True. The median of the average magnitude and direction of transport experienced by smolts that passed offshore of the array was 47.5 $m^3 s^{-1}$ 100 m^{-1} at 275.5 degrees True.

MinCnr smolts that crossed the subarray at Willapa Bay experienced an average magnitude and direction of transport of 3.51 $m^3 s^{-1}$ 100 m^{-1} at 311.7 degrees True; those that passed offshore, 45.9 $m^3 s^{-1}$ 100 m^{-1} at 278.5 degrees True. 7,503 (75%) MinCnr smolts crossed the deployed array; 1,259 of these were not detected. 2,505 (25%) did not cross the deployed array.

Sensitivity of median plume residence times to 'p_C_{max}' and switch time

Median plume residence times (PRTs) increased linearly with increasing switch time for both breeds. Median PRTs were less when 'p_C_{max}' was fixed for both

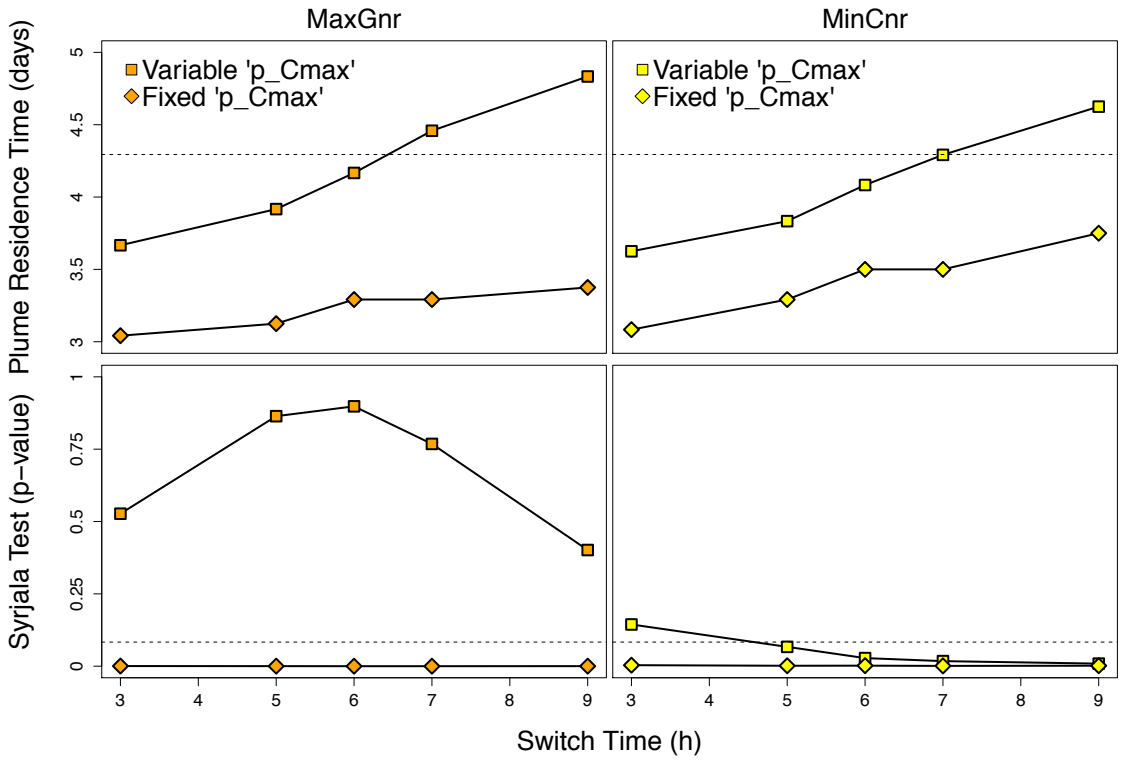

Figure 3.6. Sensitivity of plume residence time (top panels) and cross-shelf distribution (bottom panels) of both breeds to (1) the delay between reaching plume water (PSU = 27) and adopting to ocean movement rules (switch time; x-axes) and, (2) the proportion of maximum consumption assigned variably (squares) or fixed (diamonds). Horizontal dotted lines indicate observed plume residence time (top panels) and the statistically significant *p-value* of 0.05 (bottom panels). The closest match to observed plume residence and cross-shelf detections occurred in the MaxGnr breed at a 6 h switch time.

breeds than when 'p_C_{max}' was variable (Figure 3.6). The closest MaxGnr median PRT to observed median PRT occurred at a 6 h switch when 'p_C_{max}' was variable. Similarly, the closest MinCnr median PRT to observed occurred at a 7 h switch when 'p_C_{max}' was variable.

Sensitivity of the Syrjala test to 'p_C_{max}' and switch time

The Syrjala test comparing the cross-shelf distributions of observed and MaxGnr smolts was dome-shaped and not significant at all switch times tested when 'p_C_{max}' was variable (i.e., distributions were not different). When 'p_C_{max}' was fixed, *p-values* were significant and were indistinguishable across switch times. Observed and MinCnr smolts distribution tests were not significant at a 3 h switch when 'p_C_{max}' was variable (*p-value* = 0.09). They were significant at every remaining combination of 'p_C_{max}' and switch time, and indistinguishable when 'p_C_{max}' was fixed (Figure 3.5)

Discussion

The results from the individual-based model suggest that smolts pursue a strategy of maximizing growth immediately upon beginning their northward migration. Under the critical size, critical period hypothesis, which posits that adult returns are affected first by predation at marine entry, and then starvation during the first winter, this strategy could improve the probability of survival if

smolts grow to exceed the gape size of predators and attain sufficient energy reserves to avoid winter starvation. Additionally, and unexpectedly, the model indicates that strong westward transport advects smolts off the shelf; a prediction that cannot currently be validated, but could affect survival.

Pearcy (1992) noted that alongshore or offshore displacement of juveniles immediately after ocean entry could reduce predation and enhance survival. Brosnan et al.'s (2014) finding that travel time affects plume survival supports this notion. However, while it might seem that the selective use of alongshore current by the MinCnr breed would speed passage out of the plume region and enhance survival, this behavior reduced travel time to Willapa Bay by only a few hours. Applying the equation of Brosnan et al. (2014) to estimate survival to the Willapa Bay subarray using median travel times indicates that survival would be virtually indistinguishable between the growth maximizing smolts (0.60, SE = 0.05) and current minimizing smolts (0.61, SE = 0.05) that reach the array. This suggests that there is little selective pressure for the active use of alongshore-current gradients.

In addition to the apparently limited survival benefit of selective use of currents, there are additional reasons why this pattern may not extend beyond the river. First, the high density of salmon in the river raises the costs of competing for limited food resources and salmon may restrict their feeding and perform the river

migration on a limited energy budget (Quinn 2005, Cooke et al. 2011; but see Muir & Coley 1996 for evidence that smolt feeding increases in the lower Columbia River). Thus, there may be strong pressure to minimize the cost of migration in the river. Conversely, the early marine environment represents a rich feeding ground where a delay in feeding could result in smolts failing to meet the energy requirements to survive their first winter at sea (Beamish & Mahnken 2001).

Second, the confined river environment provides turbulent flow and relative motion cues from the riverbed and similar features that salmon demonstrably respond to (Standen 2004, Kemp & Williams 2005). Beyond the tidal plume, these cues are weakened. During the spring, flow in the lower Columbia River is approximately 1 m s^{-1} (and can be much greater) and exceeds 3 m s^{-1} in the tidal outflow at the river mouth, whereas ambient coastal current velocity is approximately 0.1 m s^{-1} (Hickey 1989, Jay et al. 2009). Shear turbulence is likely reduced in the coastal ocean, and smolts are not positioned to use the seabed as a frame of reference (Emmett et al. 2004). It is possible that they can detect the fine-scale changes in the intensity of turbulence and/or their motion relative to celestial objects and the earth's magnetic field. This would allow them to take advantage of small, favorable gradients in coastal current. However, they would require very sensitive absolute and differential thresholds to these cues, which have not been determined experimentally.

The successful transition from river to ocean requires that smolts complete a number of behavioural, physiological, and biochemical changes (i.e., smoltification). The precise trigger, or series of triggers, during this complex process that result in the behavioural transition to directed northward migration in the ocean have not been described. It may be driven by hormonal changes prompted by environmental cues, much as up regulation of thyroxine triggers downstream migration. We attempted to capture the transition via a simple threshold-delayed response model, but a mechanistic understanding of the process might explain why smolts are occasionally detected migrating at least as far south as Cascade Head, OR, before turning and swimming north (Rechisky et al. 2014).

Incorporating a representation of coastal feeding conditions acted to contain the MaxGnr smolts on the shelf, but the fact that nearly 20% of the MaxGnr smolts still migrated outside the bounds of the subarray at Willapa Bay is a potentially interesting result. Burke et al. (2014) report similar results, although they considered it a failure of their model and describe using an Ornstein-Uhlenbeck process that forced model fish to orient towards the historic ‘centers of mass’ of juvenile salmon sampled across the shelf in an attempt to correct it. However, trawl surveys and acoustic receiver subarrays terminate near the shelf break because few or no fish are caught in trawls near the shelf break. Results from

this model suggest that there could be a bi-modal distribution of catches/detections that would not be detected under the current sampling regime.

As Pearcy (1992) notes, this could have implications for early marine survival. Columbia River basin smolts driven off-shelf at ocean entry might experience reduced predation pressure, particularly from seabirds nesting near the river mouth (Collis et al. 2002). Their feeding opportunities would likely be reduced (Bi et al. 2007, Peterson et al. 2010), but directed northward migration would lead them to quickly regain the shelf environment, which arcs westward north of the Columbia River. Outmigrating yearling Chinook would be placed to take advantage of this offshore transport and potentially reduce their risk of predation since the necessary conditions occur in early spring, when the transition to the upwelling season is beginning and winds are strong.

A second, surprising outcome of the model was that negative rheotaxis was sufficient to guide smolts out of the estuary. The initial expectation was that the tidally-reversing flow of the Columbia River would significantly delay, or prevent, progress towards the ocean. McInerney (1964) reasoned that preference for increasing salinity could serve as an orientation mechanism for smolts in the estuary, and this mechanism was used in model development. However, when the two means of orientation were compared, they produced similar migratory patterns, although orientation by negative rheotaxis resulted in smolts initially

traveling further offshore under west transport conditions than did orientation by salinity. Negative rheotaxis was selected for the final model because it has a known biochemical basis - increasing day length stimulates the upregulation of thyroxine, which in turn causes smolts to orient with the current (Cooke et al. 2011).

Railsback et al. (1999) proposed a condition-based movement rule for stream fish in IBM's, termed *expected survival*, where fish move to habitat where the probability of surviving non-starvation mortality risks, multiplied by the probability of surviving starvation risk over a pre-determined time horizon, is greatest. Yearling Chinook in the marine environment appear to respond to feeding conditions during northward migration, so applying Railsback et al.'s (1999) *expected survival*, using the first-winter critical period as the time horizon, may be a fruitful development of the IBM presented here. This would require collaboration among researchers who have collected data on salmon predators, salmon prey, and early marine survival to develop a more accurate representation of predator and prey fields than are currently captured by the IBM. Concomitant computational and data storage demands also need to be considered[1], particularly if there is an expansion of the spatial extent of the model

[1] Prompting a variation on the Fisherman's Prayer, *"Oh funders, grant us time on a supercomputer, for the virtual ocean is so large and our laptops so small."*

ocean. Nonetheless, the knowledge and hardware are now available to bring marine fish IBMs in-line with the developments in freshwater fish IBMs, with application to understanding the effects of a changing ocean.

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CONCLUSION

In this dissertation, I have examined survival of Columbia River basin yearling Chinook salmon smolts in relation to early marine environmental processes, investigated the effect of exposure to supersaturated water on subsequent lower river and plume survival, and evaluated two potential strategies employed by smolts as they migrate through the Columbia River plume. The use of acoustic telemetry to measure survival directly, and to record migratory patterns such as travel times and cross-shelf distributions, represents an application of the technology to obtain novel insights into perennial questions in salmon early marine ecology. The contribution to the field can be summarized in the following key findings from each chapter.

Finding 1

Survival in the Columbia River plume from 2008 to 2011 can be described with a simple exponential decay model. Travel time through the plume was strongly related to sea surface temperature, although subsequent individual-based modeling suggests there may also be role for the direction and magnitude transport that was not clearly evident in the empirical data (possibly due to the grouping of smolts to estimate survival). Numerous studies have found links between survival and oceanographic variables, such as sea surface temperature, which do not have clear mechanistic effects on survival. In the plume, where predation pressures are high, travel time (i.e. the period of exposure), may be the link between such oceanographic conditions and survival.

Finding 2

Exposure to high levels of total dissolved gas below Bonneville Dam may affect survival rates in the lower Columbia River and plume. Total dissolved gas is known from laboratory studies to cause gas bubble trauma, resulting in direct mortality and indirect effects on fitness, including increased susceptibility to disease and predation. It is a widely held belief that the opportunity to compensate for elevated total dissolved gas by descending to greater depths restricts the impact of gas bubble trauma in the field. However, this has never been evaluated in a survival study, and annual field surveys clearly indicate that smolts experience gas bubble trauma during their migration. When I compared survival of smolts released at two sites below Bonneville Dam before and after TDG reached the regulatory limit, and systematically eliminated likely alternative explanations, I found evidence for survival effects of high TDG exposure in the lower river and plume.

Finding 3

Consistent with the critical size, critical period hypothesis, smolts apparently pursue a strategy of maximizing growth immediately upon beginning their northward migration. This was determined by matching patterns in the cross-shelf distribution and travel times of acoustic tagged fish with those of model fish released in an individual-based model. Minimizing head current to more quickly escape the plume environment, an alternative strategy, did not match the

patterns and offered little survival benefit to the array of acoustic receivers at Willapa Bay.

An additional observation from this individual-based model was the tendency for strong offshore westward transport to sweep smolts off the shelf. This result cannot presently be confirmed or dismissed because trawl and acoustic tracking are restricted to the shelf. If it occurs, smolts are being swept offshore where feeding conditions are poorer. However, predation pressure, particularly from seabirds nesting near the mouth of the Columbia River, may be lower offshore and north-migrating smolts would quickly regain the shelf as it arcs westward. If the critical size, critical period hypothesis is correct, there may be a survival effect, plausibly beneficial or harmful, of temporarily delaying arrival at favorable feeding grounds in favor of escaping plume predation.

Future research

The work presented here can potentially be extended in two future projects, and there are opportunities for future research developments at the intersection of acoustic telemetry and marine science.

The first extension of this dissertation work is an experimental test of the effects of total dissolved gas exposure on subsequent survival in the lower Columbia River and plume. This would address the limits of the observational study presented in Chapter 2, and should be relatively easy to accomplish. It would first

require the re-deployment of acoustic subarrays. At a minimum, these would be placed in the lower Columbia River at Astoria, and across the continental shelf at Willapa Bay and Cascade Head. Subsequently, four groups of smolts, with replicates, would be tagged. These groups include a control, and three treatment groups exposed to 110% TDG, 120% TDG, and 130% TDG, respectively. Post-exposure, the smolt groups would be released concurrently below Bonneville Dam and their survival analyzed in a similar framework to that used in Chapter 2. This study would be costly, but still relatively inexpensive when compared with the 1.1 Billion USD opportunity cost of the proposed test of spill effects on SARs in the Federal Columbia River Power System.

The second project would significantly expand on the individual-based model in Chapter 3 by incorporating the full horizontal and vertical range of the Virtual Columbia River oceanographic model, smolt mortality, and predator/prey fields with the *expected survival* movement rule. *Expected survival* calls for individuals to move to maximize survival over a given time period, trading between predation and starvation risk. Based on the critical size, critical period hypothesis, and supported by findings in Chapter 3, smolts would project their weight out to the start of their first winter at sea to estimate starvation risk. This model would require a multi-collaborator effort to access and synthesize salmon survival data from the POST project, NOAA's salmon predator and prey field sampling over decades of ocean surveys, and physical oceanographic modeling. Once complete, the model would be a useful platform for exploring the effects of

changing oceanographic and freshwater hydrological conditions on survival and migration.

More generally, understanding how a changing climate and human actions will affect salmon productivity will require a suite of observational and modeling tools. Acoustic telemetry and individual-based models are relatively novel, but hold great promise for understanding the interactions between salmon and different elements of the marine environment. As acoustic tag technology improves, and particularly as battery sizes decrease, a wider range of species, size ranges, and life histories will be accessible for direct measures of survival and migration. Marine acoustic telemetry has matured as a science, progressing from simple 'tag & track' studies to integrative research that links telemetry data with physiology. A logical pairing that has not been explored are active acoustics in biological oceanography and acoustic telemetry in marine fisheries, which could be used to investigate interactions across trophic levels.

In this dissertation, I have nudged forward our understanding of the processes affecting early marine survival of Columbia River basin juvenile yearling Chinook. The application of acoustic telemetry data to directly estimate lower river and plume survival, and to capture migratory parameters such as travel time and cross-shelf distribution, has enabled several new insights. First, survival rates are fairly constant in the Columbia River plume, and correlates of early marine survival that don't have direct effects may act on plume survival by controlling the

period of exposure to plume predation. Second, there is evidence that exposure below Bonneville Dam to total dissolved gas levels exceeding the 120% regulatory limit negatively affects survival rates in the lower river and plume. Finally, consistent with the critical size, critical period hypothesis of salmon production, it appears that smolts select habitat to maximize their growth when they begin migrating north in the coastal ocean. These findings can serve as the foundation for additional research and model development that may inform our understanding of how changing oceanography and freshwater hydrology will affect salmon migration and survival.

Appendix A

This appendix will appear as an online supplement to Chapter 2. Surgical protocols and tag effects, tag retention, and tag life studies identified in Chapter 2 are fully described in Porter et al. (2012) and briefly reviewed here.

Tag effects and retention study

In 2011, this ancillary captive tagging study was concluded after 35 days. At that time, survival, mean fork length, and mean weights of smolts implanted with V7-2L dummy acoustic tags (n = 101) and pit-tagged controls (n = 99) were not significantly different. Only one dummy acoustic tag was shed. Growth rates of the DAT-tagged smolts in 2011 were slower than pit-tagged controls, but previous, long-term captive studies conducted under the same research program suggest this effect is short-term (Rechisky and Welch 2010). Survival, tag retention, and growth effects evaluated in 2008, 2009, and 2010 studies yielded similar results.

Surgical protocol

Fish captured and identified for tagging were held in shallow tanks supplied with

river water. Food was withheld prior to surgery. Once smolts reached Stage IV anesthesia in a bath containing 70ppm Tricaine Methane Sulphonate (TMS) they were placed ventral side up and their gills gently irrigated with a water tube placed in their mouths. An incision to accommodate the tag was made on the mid-ventral line and the tag inserted into the abdominal cavity. The incision was closed with sterile monofilament absorbable suture and fish were transferred to a recovery tank before release.

Tag Lifespan Study

Forty-four V7-2L tags were randomly drawn for the tag life study from the tags available for the 2011 field study. They were exposed to the same handling conditions during the tagging period and subsequently stored and monitored in water between 18 and 22° C. The manufacturer's estimated tag lifespan was 51 days. Two tags failed prior to the rated lifespan, one on day 1, and a second on day 28. All tags expired by day 182. We used the program ATLAS methods to correct our survival estimates (Lady et al. 2012). ATLAS can apply corrections directly to CJS survival models, but not to the modified CJS survival model used in this analysis (note also that the model used in this analysis differs from the model in Porter et al. (2012)). We used Equations B.14, B.15, and B.16 from Lady et al. (2012) to implement the Kaplan-Meier method of estimating a tag survivorship curve and we used Equations B.23 through B.27 to correct each survival estimate.

Acute mortality estimate for in-river, exposed fish

At high levels of gas supersaturation (TDG > 130%), mortality due to GBT may occur within hours (acute mortality; Mesa et al. 2000). We cannot determine whether acute mortality occurred because we cannot count the number of fish that survived each day. However, if we assume that the lower river (below Bonneville) survival rate of an unexposed group represents a rate common to both exposed and unexposed groups, then the following formula can be used to estimate the acute mortality at release that would result in the observed survival to Astoria of the exposed group:

$$M_a = 1 - \left[\frac{S_{R(e)}}{S_{d(u)}^{T_{R(e)}}} \right]$$

where M_a is acute mortality, $S_{d(u)}$ is the survival rate of the unexposed group (here assumed to be common to both groups), $S_{R(e)}$ is the lower river survival of the exposed group, and $T_{R(e)}$ is the lower river residence time of the exposed group. This number can then be compared to acute mortality observed in laboratory studies at similar levels of TDG. If they are comparable, it is possible that survival rates were similar and the difference can be entirely accounted for by acute mortality occurring shortly after release; if they differ substantially, then

there is some evidence for sub-acute (chronic) TDG processes occurring that pre-dispose smolts to elevated mortality even after the acute mortality phase has passed.

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Appendix B

This appendix will appear as an online supplement to Chapter 3. This appendix describes the bioenergetics sub-model used to inform smolt habitat selection in the individual–based model described in Chapter 3.

Introduction

The bioenergetics sub-model, with 28 fixed parameters and variable inputs for smolt weight and local water temperature, is the most complex sub-model of the IBM. Its purpose is to allow model smolts to identify and then move, at a metabolically optimal speed, towards habitat (grid cells) where growth opportunities are greatest. For determining heading, it would be enough to make relative comparisons between destination cells. However, optimal swimming speed is determined in part by the weight of the smolt. Since travel time between the Astoria and Willapa Bay receiver sub-arrays is one of the patterns used in the IBM, accurate swimming speeds are desired, and thus the bioenergetics sub-model must output growth rates that are consistent with observed growth rates in the field.

Here, I identify the equations and parameter values used to build this sub-model, compare model output against growth observed in the coastal waters off the Columbia River, and report results of a global sensitivity analysis of the model parameters.

Methods

In a bioenergetics context, growth over time can be estimated using a simple mass balance equation:

$$growth = consumption - (respiration + egestion + excretion)$$

To develop the bioenergetics model for decision-making by model smolts, I used the 'Wisconsin model' bioenergetics equation sets (Hanson et al. 1997; Table 3.2) for consumption (eqn. 3), respiration (eqn. 1), egestion and excretion (eqn. 2), parameterized with values from the literature on Pacific salmon bioenergetics (Table 3.3).

To validate the model, I conducted several simulations of fish growth over 45 days. First, I fixed sea surface temperature at 8, 10, 12, 14, and 16 °C and ran the bioenergetics model in R. Then, to evaluate growth in a dynamic temperature

environment, I introduced 190 growth-seeking smolts into the NetLogo model ocean environment at random ocean locations and 10 additional smolts at random points in the lower estuary and ran the model for 45 days. In both cases, the initial length of the in-silico smolts was 150mm and their weight was 38.8 grams. I then compared the results from both simulations against low, moderate, and high growth rates of juvenile yearling Chinook observed in the Columbia River plume region from 1999 to 2008, excluding 2001 and 2005 (from Figure 5.C in Tomaro et al. 2012).

The sensitivity of bioenergetics models to their parameters is often analyzed using the 'one-by-one' approach of Kitchell et al. (1977), wherein the effect of sequentially varying each parameter input by +/- 10% of its nominal values is evaluated using equation,

$$S_x(p) = \frac{(p * \Delta x)}{(x * \Delta p)}$$

where $S_x(p)$ is the sensitivity of growth to changes in the nominal parameter p, x is growth under the nominal output parameters, and Δp and Δx are changes in the nominal input parameters and nominal growth, respectively.

However, this approach does not capture the combined effects of varying more than one parameter (Rose et al. 1991, Hamby 1994, Megrey et al. 2002). To conduct such a 'global' sensitivity analysis, I drew 10,000 random Latin Hypercube parameter combinations and evaluated, for each parameter, the correlation between value of the input parameter and the final weight (Megrey et al. 2002), and whether the final weight from each combination was within the range of smolt growth calculated using rates reported in Tomaro et al. (2012). The parameter space from which each parameter was drawn was +/- 10% of the selected parameter values in Table 3.3, except that the proportion of maximum consumption, 'p_C_{max}', ranged from 0 to 1 (Beauchamp et al. 1989, Brodeur et al. 1992, Railsback and Rose 1999, Beauchamp et al. 2007) and prey energy density, Q_f, ranged from 2800 to 5000 (Muir et al. 2006, Trudel et al. 2005, Beauchamp et al. 2007). Four parameters were fixed; the water temperature (T = 10 °C), the cutoff water temperature at which the activity relationship changes (RTL = 25 °C), the intercept for swimming speed above the cutoff temperature (RK1 = 1 cm s^{-1}), and the conversion parameter *c* used to convert the kJ g^{-1} output of Trudel et al.'s (2005) predator energy density model to the J g^{-1} input required by the Wisconsin model equations (*c* = 1000).

Results

The literature on Chinook salmon bioenergetics provided a relatively rich pool of parameter values for the bioenergetics model (Table 3.3). Simulations in R

(Figure B.1) and in NetLogo (Figure B.2) produced growth consistent with rates observed in coastal waters.

The model was most sensitive to changes in the consumption parameters, particularly the proportion of maximum consumption, 'p_C_{max}'. These results are consistent with the findings of Stewart et al. 1983 and Beauchamp et al. 1989 (following Kitchell et al. 1977), as well as Railsback & Rose (1999). Of the parameters that the model is sensitive to, specifically prey energy density and proportion of maximum consumption, the values in the literature produce results consistent with the range of observations in Tomaro et al. (2012). For example, 'p_C_{max}' is never reported in the literature as less than 0.2 and the sensitivity analysis suggests that, given the observations of Tomaro et al. (2012), 'p_C_{max}' would not be less than 0.2 (Figure B.3)

Discussion

Bioenergetics models are grounded in the law of conservation of energy, which states that the energy in an isolated system can be transferred, but total system energy cannot change. From this, it can be shown that the consumption by a fish must be balanced by its growth, respiration, egestion, and excretion. This formula

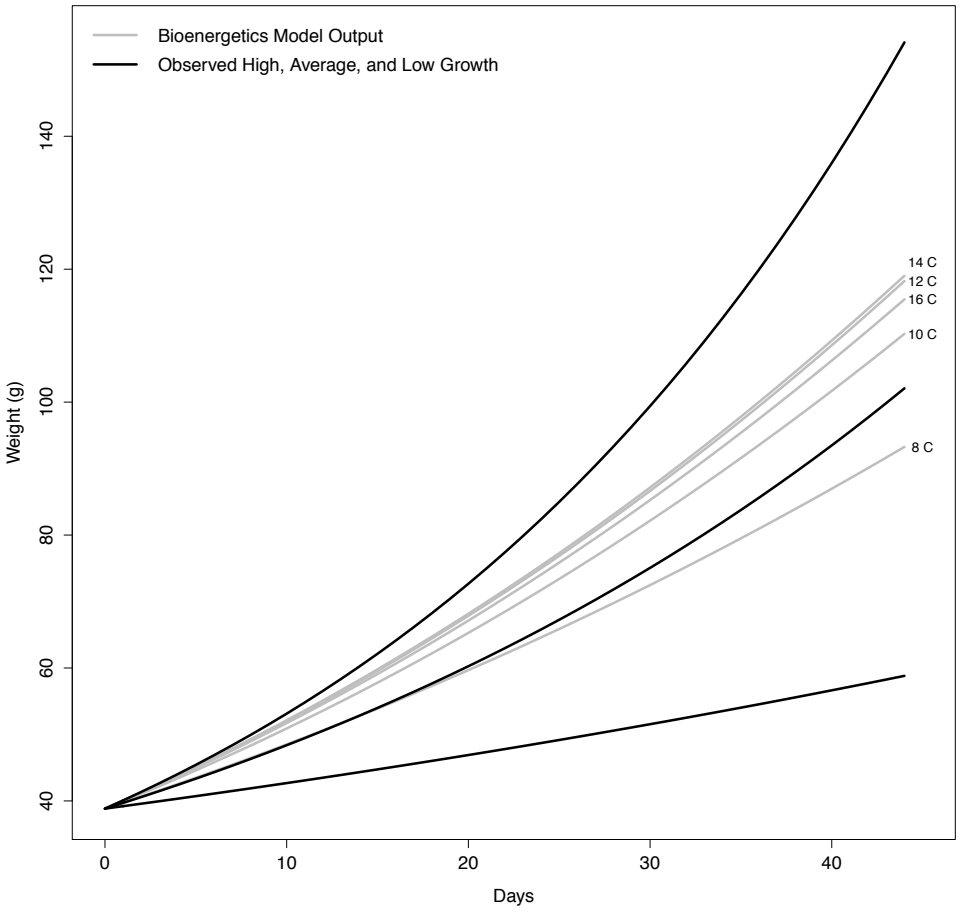

Figure B.1. Growth curves for smolts at five simulated temperatures (grey lines) and growth curves representing the high, low, and medium growth rates observed in coastal waters (black lines).

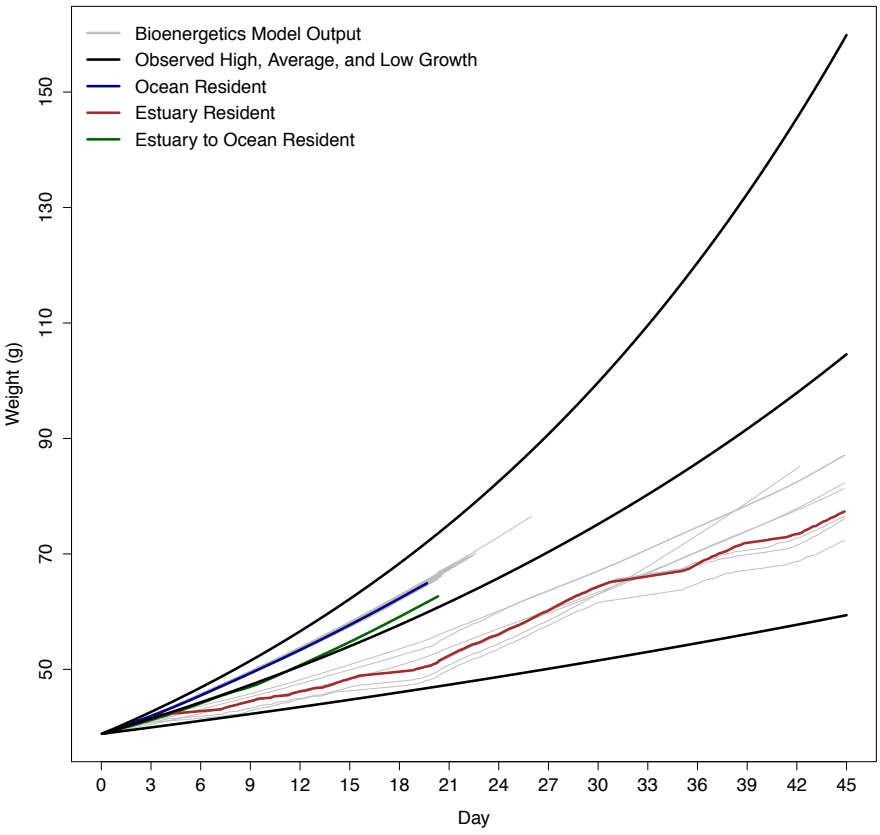

Figure B.2. Simulated growth of model smolts in the VCR-derived model ocean. Colored lines are exemplar model smolts that were initialized in the ocean (blue) or initialized in the estuary and either migrated to the ocean (green), or failed to leave the estuary (brown). Growth curves end where smolts emigrated from the model world. Black growth curves representing the high, low, and medium growth rates observed in coastal waters.

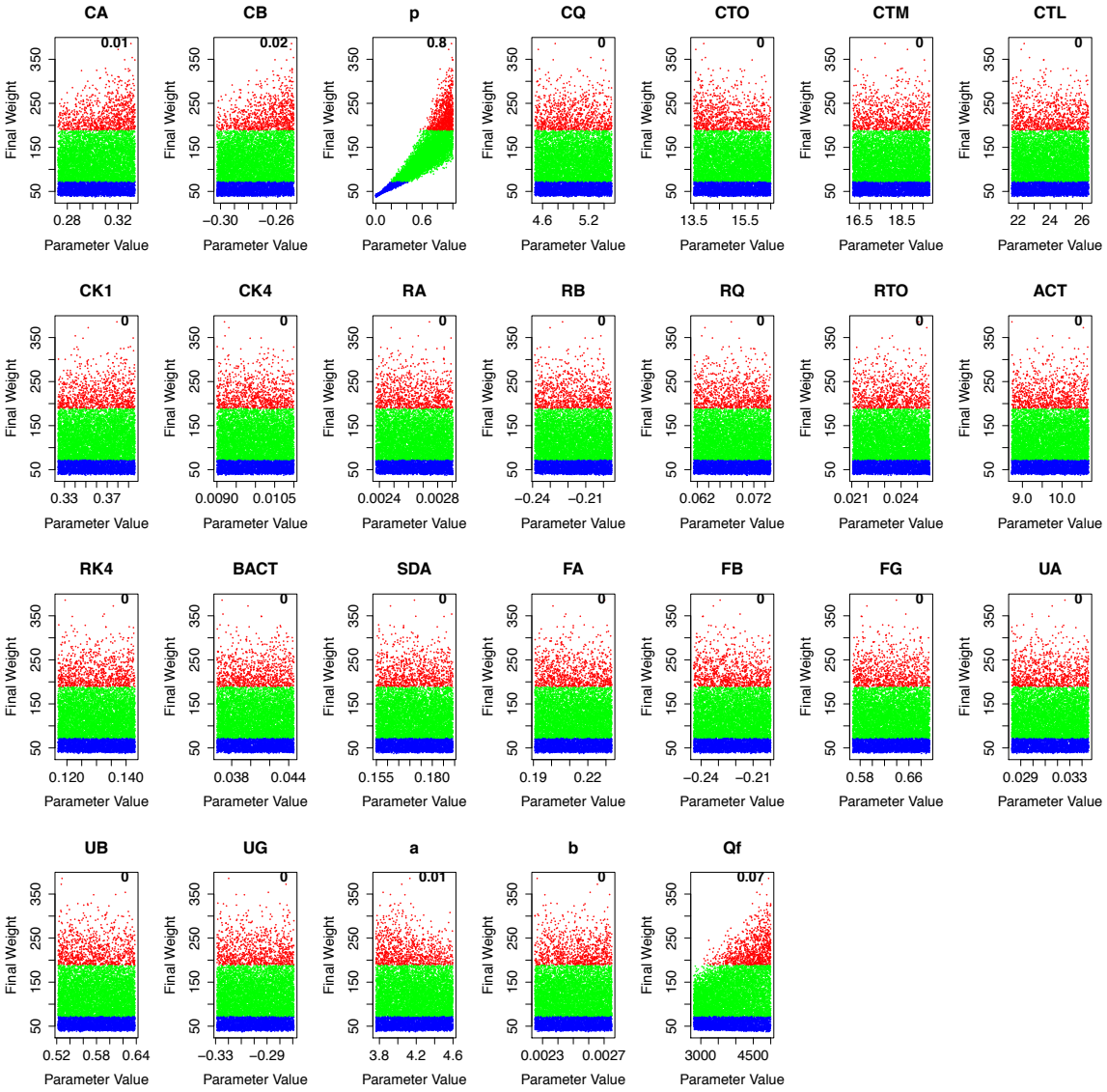

Figure B.3. Latin hypercube sensitivity analysis of bioenergetics parameters. Colors indicate whether final weight exceeds (red), meets (green), or is below (blue) growth consistent with observations reported in Tomaro et al. (2012). Bold numbers in the top right of each panel are R^2 values indicating sensitivity of observed growth to the change in parameter values. Parameter definitions can be found in Table 3.3. Growth appears sensitive only to changes in the proportion of maximum consumption and, to a lesser extent, energy density of prey.

is commonly used to estimate growth or consumption with empirically derived equations and parameters, the most popular of which are probably the 'Wisconsin model' equation sets used in the Fish Bioenergetics software (Ney 1993, Hanson 1997). These equations can also be used as the basis for movement rules in individual-based models (IBM's; Grimm and Railsback 2005).

Bioenergetics models have been subject to some criticism due to the uncertainties in model formulation and parameter values, the practice of 'parameter borrowing' that occurs as a result of the difficulty of parameterizing the models for new species, and application of the models in environmental conditions different from those used to develop the original model parameters (Ney 1993, Beauchamp et al. 1989, Railsback and Rose 1999, Trudel et al. 2005). Fortunately, model parameters reported for Pacific salmon in the Great Lakes (e.g., Stewart 1980) have been refined for Pacific marine waters (Beauchamp et al. 1989, Trudel et al. 2005, Beauchamp 2007) and our simulations of growth using these parameters produce estimates that fall comfortably within the range of growth rates observed in the marine waters off the Columbia River by Tomaro et al. (2012). Similarly, and reassuringly, Brodeur et al. (1992) also found good correspondence between observed growth and bioenergetics model predictions of juvenile Pacific salmon growth in the early-1980's.

Weight-dependent, metabolically optimal cruising speeds are generally considered appropriate for pelagic, migrating fish such as juvenile salmon (Hinch and Rand 2000); good correspondence between modeled growth and observed growth suggests that we are assigning individual fish an accurate weight, and therefore speed. However, this requires the assumption that juvenile salmon generally travel at such metabolically optimal swimming speeds, as opposed to burst and rest patterns of feeding and predator avoidance.

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